BULLETIN
OF THE
TORREY BOTANICAL CLUB

VOLUME 68 MAY 1941 NUMBER 5

STUDIES IN THE GENUS PHYSALACRIA[1]

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(WITH ONE HUNDRED AND FIVE FIGURES[2])

The genus *Physalacria* is generally regarded as a member of the family *Clavariaceae* (Killerman in Engler and Prantl 1928; Coker 1923; Clements and Shear 1931), although more recently the suggestion that it be transferred to a place amongst the *Thelephoraceae* has been advanced (McGuire 1939). This proposal is based upon the assertion that the hymenium occupies a unilateral and inferior positon instead of being amphigenous, which is the usual hymenial characterization for the *Clavariaceae*. McGuire has convincingly demonstrated the fallacy of the amphigenous distribution in *Physalacria* and has pointed out also the erroneous conclusions of previous investigators who followed this assumption. Up to now very little attention has been devoted to detailed studies of any of the *Clavariaceae*. Wakyama (1932) mentions the basidia of *Clavaria* briefly, but only as a prelude to studies never completed. A comprehensive treatment of *Typhula* has just appeared (Remsberg 1940), but without the inclusion of cytological data. Apparently *Physalacria* has not been investigated cytologically. In order to ascertain with any certainty the approximate positon of this genus and its relationships, a complete study of the basidiocarp development and differentiation seems necessary.

Despite the fact that this genus has been defined clearly enough for recognition for over fifty years (Peck 1882), collections of this attractive little genus are still infrequent. A number of collections have been made in the intervening years, chiefly in the eastern part of the United States and Canada. The material serving as a basis for this study was collected July 25 and July 27, 1935, from basidiocarps growing on a decaying stump in Door County, Wisconsin. At that time the fructifications were prolific but in subsequent seasons they failed to appear although the stump was carefully watched during the summers of 1936 and 1938. The summer of 1936 was an

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[2] The publication of the illustrations was assisted by a grant from the Lucy Maynard Salmon Research Fund of Vassar College.

[THE BULLETIN FOR APRIL (68: 207–264) WAS ISSUED APRIL 1, 1941]

exceptionally dry one but even after the beginning of the rainy season the fungus did not reappear.

The material was fixed and preserved in formol-acetic-alcohol. Later characteristic stages of development were selected for sketching, and, in turn, sectioning. All material was dehydrated in a butyl-alcohol series previous to imbedding, and serial sections 3, 5, 8, and 10 μ thick were cut. Slides were stained with Heidenhain's iron-alum-haematoxylin and counter-stained with phloxine. Temporary mounts were examined in a lacto-phenol preparation with a combination of cotton-blue and acid fuchsin as stains.

The youngest stage sectioned revealed a scarcely differentiated ball of tissues partially imbedded in the wood cells of the substratum (fig. 1). Hyphal filaments with no special orientation abundantly pack the lumens of the wood cells at this and later stages (fig. 2). The hyphae appear to be binucleate. Basally the filaments are compactly arranged, forming a zone of thin-walled pseudo-parenchyma (fig. 3). Inside the hyphal cells the cytoplasm forms a scant lining, and the nuclei, when apparent, are in close association or are scattered. Above the basal tissue the hyphae often appear as longer cells although their pseudo-parenchymatous nature is not lost completely (fig. 4). A short distance below the surface of the basidiocarp the cell arrangement becomes briefly reticulated before passing into the long loose hyphae which radiate freely over the surface. The hyphal tips are completely undifferentiated (fig. 5).

When the distinction between stalk and head of the fructification is first visble, the tissues are fundamentally the same as in the button stage although they are now present in larger amounts (figs. 6, 7). Active cell division in all parts of the developing basidiocarp allows for its growth and subsequent tissue differentiation. The enlarging head is formed of reticulate filaments and free surface hyphae. Already much elongated at this stage, the stalk is composed of cells with nuclei in active divsion as well as in conjugate pairs

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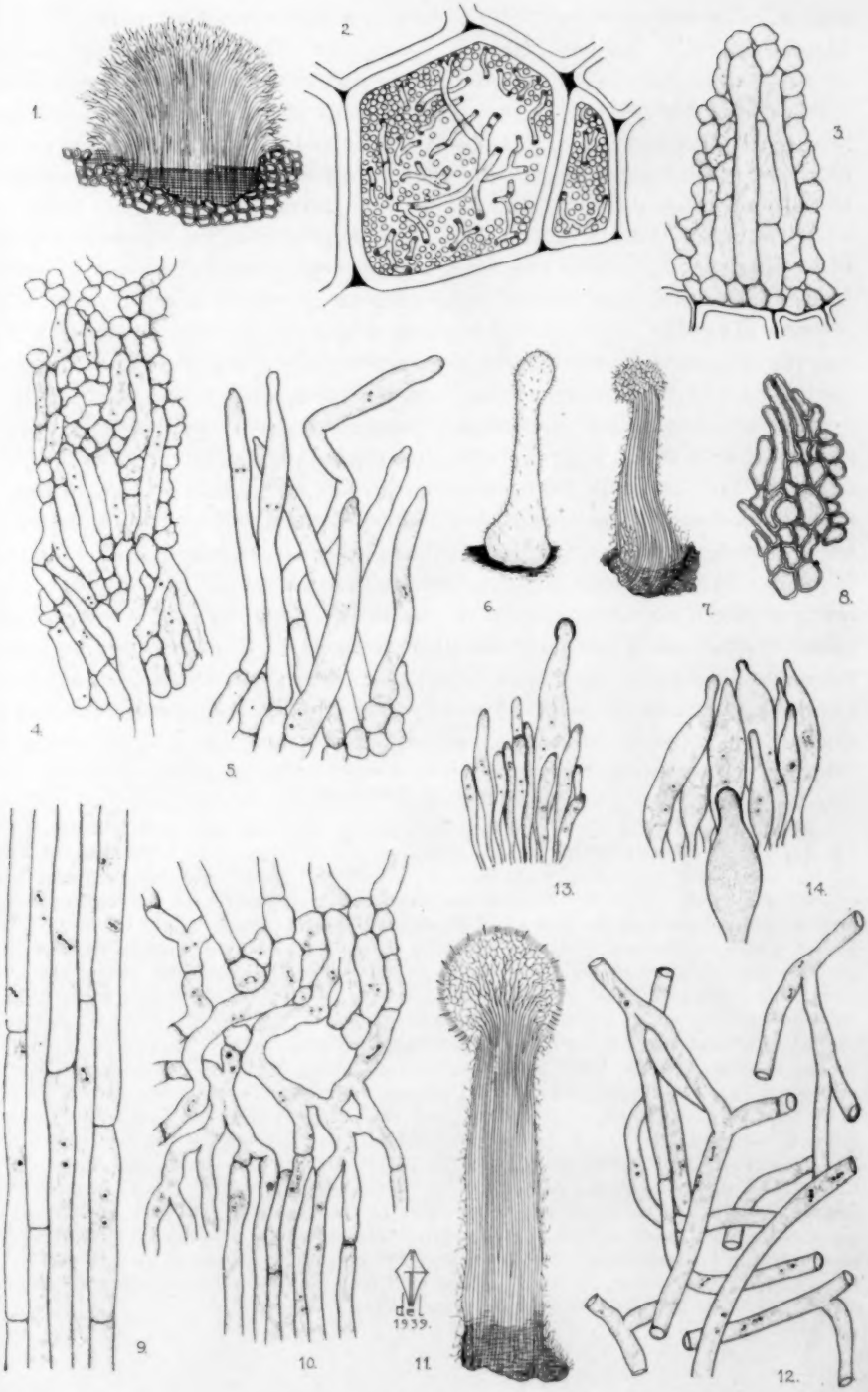
Explanation of figures 1–14

All figures were drawn with the aid of an Abbé camera lucida.

Physalacria inflata. FIG. 1. Section of a young basidiocarp growing on wood. Diagrammatic. ×47. FIG. 2. Detail of wood cells of substratum showing the lumens filled with fungous hyphae. ×550. FIG. 3. Cells from pseudo-parenchymatous zone at base of the basidiocarp illustrated in fig. 1. ×937. FIG. 4. Cells from the interior of the basidiocarp shown in fig. 1. ×937. FIG. 5. Free hyphae from the surface of the same basidiocarp. ×937. FIG. 6. Habit sketch of a young basidiocarp, the head region barely distinguished. ×18. FIG. 7. Section of basidiocarp shown in fig. 7. ×20. FIG. 8. Basal cells of basidiocarp of fig. 7. Note thickening of walls. ×937. FIG. 9. Stalk hyphae from same basidiocarp. ×1550. FIG. 10. Cells from the region of junction between head and stalk. ×937. FIG. 11. Diagrammatic view of a longitudinal section through a developing basidiocarp. ×47. FIG. 12. Reticulate hyphae from the head of the basidiocarp in fig. 11. ×937. FIG. 13. Hyphae from the surface of a young basidiocarp in the future fertile area. ×937. FIG. 14. Hyphae from the surface of a young basidiocarp in the future sterile area. ×937.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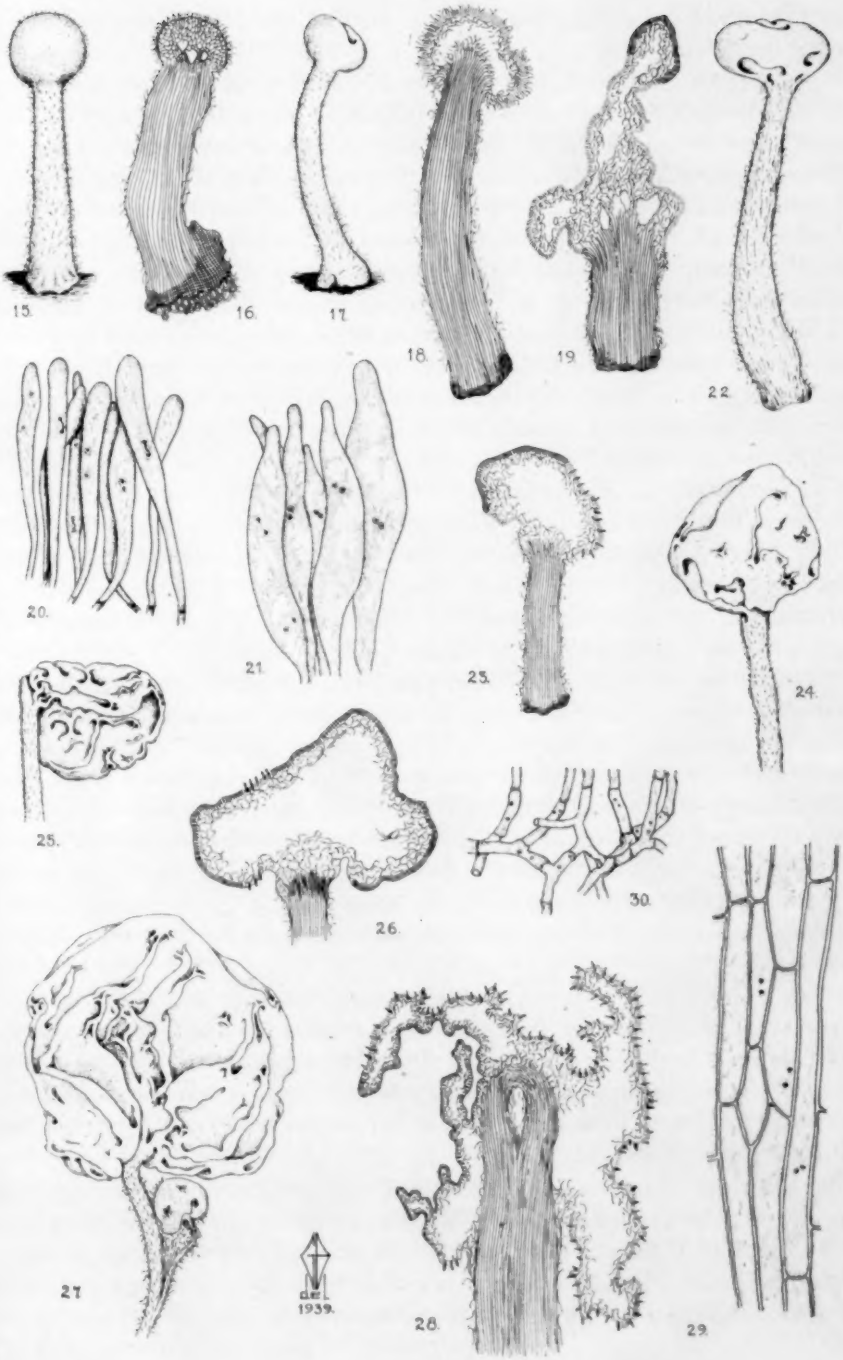
(fig. 9). The cells are thin-walled, elongated, and mostly are arranged in a compact parallel fashion, although occasionally they are branched. Those toward the outside often are of greater diameter than the internal ones. The walls of the pseudo-parenchymatous cells at the base of the stalk are slightly thickened (fig. 8). In a succeeding stage in the region where the head and stalk tissues adjoin, the reticulate portion becomes much anastomosed and consequently is difficult to trace. Here, too, the nuclei are commonly found to be dividing (fig. 10). The bulk of the head is a loose reticulum of hyphae (fig. 12) which now supports a compact layer of cells on the surface; this results in a smooth head without gyrations (figs. 11, 15). The peripheral hyphae lie parallel to each other in a palisade arrangement. They may be of unequal lengths, but they are usually binucleate and are supported basally by a layer of more closely interwoven cells. In places the hyphal ends are inflated and show a decreasing cytoplasmic content; these are young cells which later will comprise the bulk of the sterile tissues of the head. Cells of the fertile parts are much smaller, filled with dense cytoplasm, and are more or less clavate in shape. Sterile and fertile areas consequently become recognizable long before the basidiocarp is morphologically mature (figs. 13, 14). Occasional cells may have already matured into cystidia, and a few of these may be emergent, but many of them are still disposed well within the tissues. Externally the stalk, from its earliest inception, appears tomentose because of many such inflated cells which terminate free marginal hyphae along its entire length. These hyphae are identical in appearance and nuclear history with the inflated cystidia of the cap (figs. 58, 59). Possibly

Explanation of figures 15–30

Physalacria inflata. FIG. 15. Young basidiocarp with head and stalk distinct. ×47. FIG. 16. Section of same basidiocarp in diagrammatic longitudinal view, showing the first separation of reticulate tissues in the head. ×50. FIG. 17. Older basidiocarp showing first external fold in the cap. ×15. FIG. 18. Section of basidiocarp of fig. 17, diagrammatically represented, and showing the first complete separation of the tissues inside the head. ×14. FIG. 19. Older basidiocarp showing progressive separation of internal tissues. Section diagrammatic with future hymenium restricted in this section to upper lobe. (Other sections show other lobes as fertile.) ×14. FIG. 20. Hymenium from fig. 19. Cross-walls are infrequent and the nuclei are in active division at this stage. ×1550. FIG. 21. Surface hyphae which comprise sterile areas of the same basidiocarp; the largest cell is a cystidium. ×1550. FIG. 22. Developing basidiocarp showing infolding on upper and lower surfaces. ×15. FIG. 23. Section of basidiocarp of approximately same age as that shown in fig. 22, with complete separation of cap and stalk tissues; the hymenium occurs on the left side and partly covers the upper surface. ×14. FIG. 24. A mature basidiocarp. ×0.75. FIG. 25. Mature basidiocarp strongly lateral in the attachment of cap and stalk. ×1.2. FIG. 26. Diagrammatic section of basidiocarp shown in fig. 24. ×47. FIG. 27. Completely matured basidiocarp with younger one connate at the base. ×2. FIG. 28. Section of a much inflated and lobed mature basidiocarp. In this section the fertile area is on the left margin but in other sections fertile areas occurred on the right lobes and not on the left. Diagrammatic. ×47. FIG. 29. Stalk hyphae with thickened walls from a mature basidiocarp. ×550. FIG. 30. Detail of subhymenium. ×937.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they should be designated caulocystidia, sensu Buller, but such a distinction seems unnecessary here.

As internal differentiation progresses conspicuous openings appear in the cap immediately above the termination of the stalk hyphae (fig. 16). Later these become confluent and through more extensive growth make the first separation between cap and stalk tissues (cf. figs. 17, 18, 19). The surface hyphae are at this time approaching their ultimate size and arrangement (figs. 20, 21). The hymenium consists of closely parallel hyphae whose slender clavate tips contain dense cytoplasm and whose nuclei are either undergoing karyogamy or are in varying stages of division, presumably meiotic. The fertile hyphae are supported by a subhymenial layer of loosely interwoven cells. No mature basidia are to be found at this stage. Cross walls are infrequent, so that often two sets of nuclei appear in one hyphal end. However, the hymenial distribution is well-marked, because the sterile surface hyphae are larger, fusiform, and more vacuolate than the fertile tips. Ventricose cystidia are prominent in this tissue. Some are not emergent and their nuclei are commonly in karyogamy or in the first meiotic division. Those which do project are usually binucleate, having resulted from fusion and one division. Nuclei in both the subhymenium and the underlying reticulum of the cap are still actively dividing. Such division allows for the continued expansion and inflation of the cap.

Just before the maturation of the hymenium the cap shows externally the first conspicuous folds, predominantly on the lower side, and internally the complete separation of the cap from the stalk (figs. 22, 23). Projecting cystidia of two types occur over the head: large ventricose ones which have a thickened rostrate head and slender fusiform ones which may or may not have thickened tips. They are all binucleate. Apparently these cystidia reach maturity in advance of the basidia and the surface cells of the sterile zones; the nuclei of the two latter cell-types being mostly in karyogamy or the division thereafter. Stalk and subhymenial cell nuclei are likewise often in division.

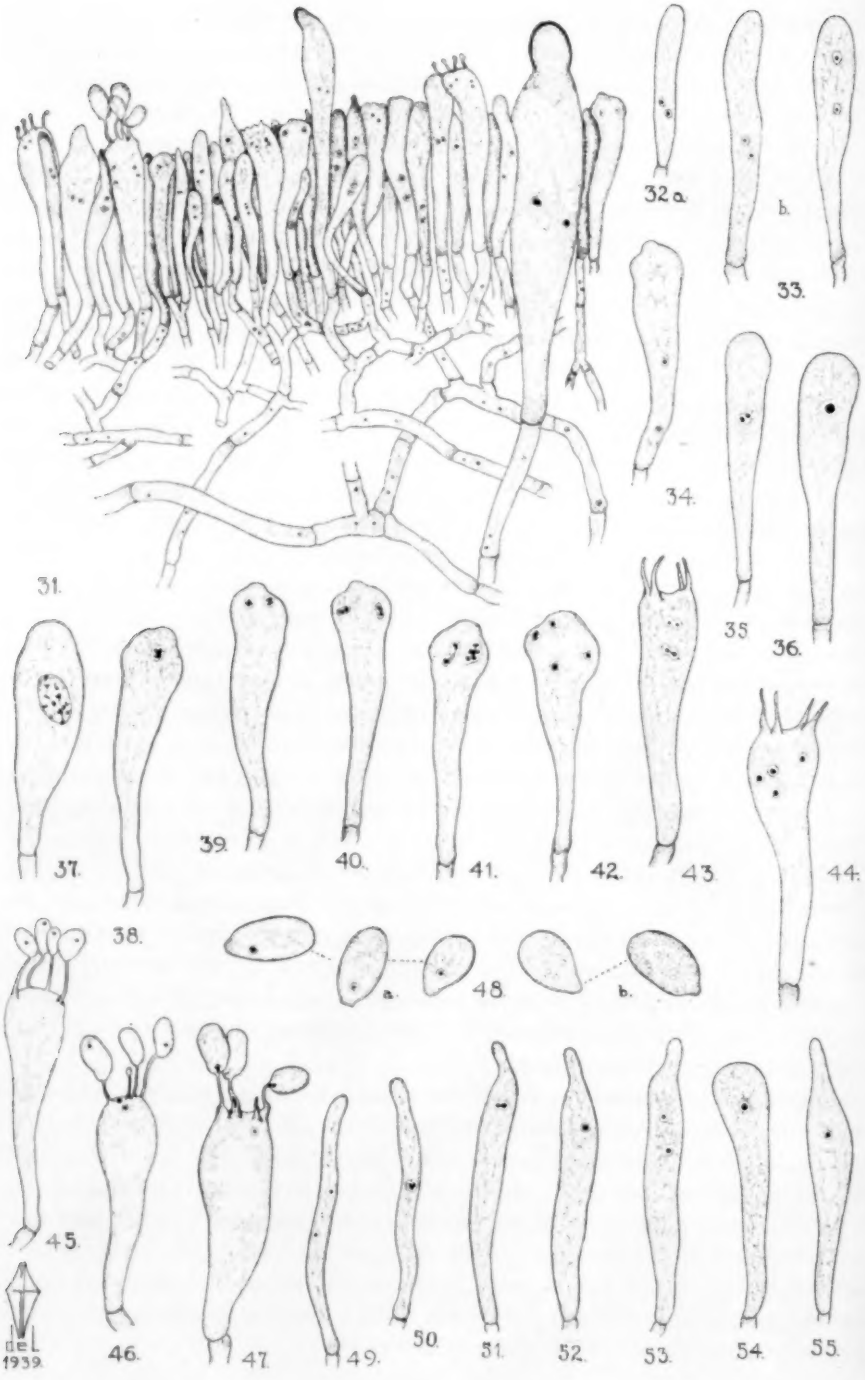
The mature basidiocarp has clearly distinct fertile and sterile surface areas. According to its age it is more or less convolute and inflated. The infoldings are due to the expansion of the cap tissues, both fertile and sterile. In section a basidiocarp of external appearance, such as that shown in figure 24, has a hymenial layer about 20 μ thick, supported by the subhymenium ranging from 10–15 μ in thickness (fig. 30), both of which are supported from below by a zone of loose reticulate hyphae from 50–150 μ deep. The sterile portions, which are from 30–40 μ thick, rest directly on the reticulum. The remainder of the cap is entirely hollow except in the region of the stalk, where the parallel hyphae may protrude into the hollow, although generally these tissues are covered by a few reticulate strands (fig. 26). The stalk tis-

sues may be confluent with the reticulum of the cap when the lateral attachment of the stalk is extreme or the convolutions are highly irregular (figs. 25, 28). It is evident that although collapse of the bladder may explain some irregularities of the cap, the foldings are usually due to differences in expansion, for the cell layers show no signs of shrinkage or distortion.

When completely mature the basidiocarp is extremely convoluted and greatly expanded (fig. 27). The walls of the mature stalk cells are much thickened, the cytoplasmic content is reduced, but the nuclei are still prominently associated in pairs (fig. 29). The distribution of the hymenium is variable but never amphigenous. A detailed examination of the hymenium from a section of the basidiocarp illustrated in figure 24 reveals that it is composed of basidia, paraphyses, and cystidia (fig. 31). The surface of the sterile part is made up entirely of fusiform, expanded cells. Altogether four kinds of sterile elements may be distinguished in *Physalacria*. McGuire (1939), who mentions the large ventricose cystidia and smaller, slender fusiform ones, described their form and position correctly. Both occur over the entire head, but more abundantly in the sterile portions. Ventricose cystidia, which are conspicuous for their thickened rostrate heads and their enormous size (26–52 × 4–10 μ) project from 9 to 30 μ above the surface. Fusiform cystidia, 40–50 × 4–6 μ, occur freely in the sterile portions, and less frequently in the fertile tissue than the ventricose type. Furthermore, the fusiform ones are often found in greatest numbers in the transition region between fertile and sterile areas. This difference in distribution may be seen in diagrammatic representation (fig. 100). The fusiform type is further distinguished in that it projects farther, as much as 50 μ, and is always emergent. Occasionally the tip is thickened. Both kinds of cystidia are comparatively full of cytoplasm and are binucleate.

Besides the cystidia there are the cells which constitute the bulk of the sterile surface layer. These are fusiform cells of an intermediate size, 24–31 × 4–9 μ; their free ends are never thickened, however, and they are united in a compact upright layer. None of them projects beyond the surface, although, being somewhat variable in length, they form a slightly uneven surface. Their extreme vacuolation is most conspicuous and from most of them the nuclei have disappeared.

Amongst the basidia are found the much smaller paraphyses, which are also non-emergent, unencrusted cells. Figures 31 and 56 illustrate these sterile and fertile elements, drawn to a common scale. The hymenium rests on the subhymenium, which consists of small hyphae, 1–2 μ in diameter, more or less upright in position, parallel for the most part, but occasionally branched and interwoven. This layer is supported from below by the cells of the reticulum, which are coarser, 2–4 μ in diameter, and definitely intertwined. All of its cells are binucleate with irregular cytoplasmic content. The subhymenium is lacking in the sterile parts.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Basidia usually arise as terminal hyphal cells, and develop in series. Consequently in any given portion of the hymenium stages of development may range from very young basidia with unfused nuclei to mature basidia which are slightly emergent at the time of spore discharge. Cytologically the development of the basidium is that any typical homobasidum. Even when very young the basidia are comparatively distinct from the paraphyses, for they are shorter and more clavate as early as the pre-fusion stage (cf. figs. 54 and 55). The young basidium is densely protoplasmic and binucleate (fig. 32). By the time nuclear fusion has taken place it has already enlarged considerably, and become slightly vacuolate. Before fusion the nuclei lie midway in the cell. As the basidium enlarges the nuclei also increase in size (fig. 33). The basidium is well on its way to maturity before karyogamy occurs (figs. 34, 35). At the time of fusion the two nuclei move near the enlarged end (fig. 36). Here fusion takes place and is soon followed by the prophase of the first division, which is probably meiotic (figs. 37, 38). The basidium continues to enlarge at the outer end. The second division follows at once (figs. 39, 40), although the division of the two daughter nuclei is not necessarily simultaneous (fig. 41). At the four-nucleate stage the basidium is decidedly enlarged and near its maximum size. The four nuclei lie toward the outer surface (fig. 42). Sterigmata then appear, growing to a length of 1 or 2 μ before the spore vesicles begin to form (figs. 43, 44). As the sterigmata and spores develop the basidium becomes correspondingly more vacuolate. The nuclei move near the sterigmata, pass through them into the spores in an attenuated mass, and finally are reorganized within the young spores

Explanation of figures 31–55

Physalacria inflata. FIG. 31. Detail of mature hymenium, subhymenium, and a portion of the reticulate hyphae. × 1250. FIG. 32. Young basidia, pre-fusion. × 2060. FIG. 33. Older basidium, pre-fusion. × 2060. FIG. 34. Older basidium, pre-fusion. × 2060. FIG. 35. Basidium with fusing nuclei. × 2060. FIG. 36. Basidium with fusion nucleus. × 2060. FIG. 37. Basidium with nucleus in prophase of first post-fusion division. × 2060. FIG. 38. Basidium with nucleus at end of first post-fusion division. × 2060. FIG. 39. Basidium, two-nucleate, the nuclei in the second post-fusion division. × 2060. FIG. 40. Basidium with nuclei near the end of the second post-fusion division. × 2060. FIG. 41. Basidium with two nuclei in division, one nucleus in advance of the other. × 2060. FIG. 42. Four-nucleate basidium. × 2060. FIG. 43. Basidium with four sterigmata and four nuclei approaching end of second division. × 2060. FIG. 44. Basidium with four sterigmata previous to spore formation. × 2060. FIG. 45. Four-spored basidium, the spores immature. × 2060. FIG. 46. Basidium with developing spores, two nuclei still in the basidium. × 2060. FIG. 47. Basidium with three mature spores and one nucleus passing through the sterigma. × 2060. FIG. 48. *a*. Mature spores from permanent slides. × 2060. *b*. Spores from a fresh mount. × 2060. FIG. 49. Young paraphysis from fertile zone, pre-fusion. × 2060. FIG. 50. Paraphysis from fertile zone, the nuclei fusing. × 2060. FIG. 51. Paraphysis with nucleus dividing. × 2060. FIG. 52. Mature uninucleate paraphysis. × 2060. FIG. 53. Mature binucleate paraphysis. × 2060. FIG. 54. Uninucleate post-fusion basidium. × 2060. FIG. 55. Uninucleate post-fusion paraphysis from the same preparation as fig. 54, and adjacent to the basidium figured there. × 2060.

(figs. 45, 46, 47). Spore formation and nuclear migration are not always simultaneous in the same basidium (fig. 47). The spores are apparently uninucleate. In only one did two nuclei appear to be present. Peck (1882) claimed that the basidia were two-spored. Neither fresh mounts nor serial sections confirmed this statement. One basidium, already past spore-bearing, seemingly had two nuclei still in the cell, which was almost devoid of cytoplasm; one of these nuclei likewise seemed to be disintegrating. If so, it may be that when and if two-spored forms occur the extra nuclei degenerate.

In the development of the paraphyses in the hymenium it appears that their nuclei go through karyogamy, after which one division may occur, although commonly there is no further nuclear change after fusion (figs. 49–53). Mature uninucleate paraphyses are readily separable from uninucleate basidia by reason of form and size (figs. 54, 55). Fusiform cystidia usually undergo one division after fusion of their nuclei and then remain conspicuously binucleate (figs. 57–59).

The cells which comprise the sterile layer arise in the same manner as basidia: from the ends of hyphal filaments. As soon as the cap is distinguished from the stalk, but long before its tissues are mature, it is possible to recognize the hyphae which become the cells of the sterile regions and those which will become the hymenial layer. Th former are definitely larger, more fusiform, and less densely filled with cytoplasm. The sterile cells mature in advance of the basidia, as has been already pointed out. Nuclear fusion occurs here as in the cystidia and basidia and is then followed by one division (figs. 60–62). No subsequent division was noted and in mature basidiocarps these cells quite commonly have no nuclei. Since chromosomal elements are too small to distinguish as units, it is impossible to say whether the one division that follows fusion in the sterile cells is meiotic.

In any part of the fructification the ventricose-rostrate cystidia are the most striking elements. Their nuclear history is clearly defined. The nuclei of the dikaryon enlarge, come together, and thereupon the membrane breaks down at the point of contiguity (figs. 63, 64). A large fusion nucleus results which proceeds from a conspicuous prophase (fig. 65) through successive karyokinetic stages, and ends with the return of the binucleate condition (figs. 66–68). Further division does not seem to occur and the two nuclei remain more or less central in the cystidium. No indication of future disintegration was noted, although the cytoplasm becomes more vacuolate with maturity.

Obviously the variation which attends the formation of the sterile cells is more striking than the already well-known pattern of the basidium development. Cytological studies dealing with the sterile elements of the basidiomycetes are relatively few. Whelden (1936) cited what literature there is on the subject when he published an account of cystidial and gloeocystidial be-

havior in a species of *Peniophora*, one of the *Thelephoraceae*. Whelden traced the nuclear changes in cystidia from the fusion of the dikaryon nuclei through one division of the fusion nucleus. After this the nuclei disintegrate and later disappear completely. The development of the gloeocystidia remains obscure because of their dense content. However, gloeocystidia are definitely distinguished from cystidia because they arise as lateral branches of the deeper hyphae of the mycelium and not as hyphal tips, from which the cystidia are formed.

In *Physalacria* there are four distinct types of sterile cells, already described. Of these three types take their origin from hyphal tips: namely, the paraphyses found amongst the basidia, the projecting fusiform cystidia, and the inflated fusiform cells of the sterile tissue. Although all these have a common origin their subsequent history is not identical; but in none of them does nuclear development proceed beyond one division of the fusion nucleus. It would be interesting to know the exact nature of this division, whether it is meiotic or not, but the nuclei are too small to permit chromosome counts. The origin of the ventricose-rostrate cystidia is various. At times it is distinctly from a terminal cell, but when the cystidium remains disposed internally within the reticulum it may arise from a lateral cell. In these fusion and one division thereafter are clearly demonstrable.

The first three types of cystidia are comparable in their origin to a basidium, though morphologically they are distinct in early stages of development. Certainly the ventricose-rostrate cystidia are distinct from the beginning. Their origin, even when terminal, seems to be associated with the internal tissues and since they do not take their origin from surface cells it is likely that their primordia are not comparable to the basidial primordia. They would appear to be modified cells of the internal mycelium, some of which push through the surface layers to the outside, and some of which remain inside. Krieger (1923) referred to these ventricose cystidia as "ducts," but nothing to support this contention was observed.

As McGuire (1939) has stated, the determination of fertile and sterile areas is relatively obvious, owing to the more compact appearance of the basidial layer and the greater frequency of the projecting cystidia in the sterile parts. Twelve basidiocarps of mature differentiation were sectioned serially and compared for hymenial distribution. From these it was apparent that little if any regularity pertains to the distribution of the hymenium. McGuire found experimentally that the basidiocarps do not invariably grow erect, but the hymenium may be directed downward. In the material used here six basidiocarps had hymenium only on the lower surfaces near the stalk, and none on the upper surfaces (fig. 101). It may be assumed that these six grew more or less upright. Three had the hymenium predominantly situated on the surfaces away from the stalk. Their position might have been

inverted or lateral (fig. 103). One basidiocarp had the hymenium spread irregularly over all portions of the cap, sometimes even amphigenously in single sections, though one lateral aspect was intermittently fertile, and hence may have grown slightly obliquely (fig. 102). Another basidiocarp had a hymenium so scattered in all parts that its position might have been only slightly lateral, or almost erect (fig. 105). Three connate basidiocarps displayed in section both under and upper surfaces fertile (fig. 104). To such basidiocarps McGuire's statement that the hymenium invariably "occupies the portion of the head which is actually turned downward" could not apply. It seems that the most definite conclusion one can draw is that the hymenial distribution is highly irregular and that it is never completely amphigenous over the surface of the cap, but that apparently there is a predisposition for the under surfaces to be fertile.

TAXONOMIC POSITION

Ordinarily the family *Clavariaceae* is classified between the *Thelephoraceae* and the *Hydnaceae*. As usually defined the family includes genera whose erect sporocarps are either simple or branched in varying degrees of complexity. The hymenium covers "most of the plant, usually all except a more or less well defined base or stem, which may fade imperceptibly into the upper part or be more or less delimited by a change in size or color" (Coker 1923). Nearly all taxonomic treatments summarize this diagnosis by saying briefly that the hymenium is amphigenous. If such a criterion is to be applied without any latitude, *Physalacria* will be excluded from the family.

But the confusion which has attended the understanding of the genus *Physalacria* extends to the family as a whole. Distinctions amongst the comparatively few genera included in the *Clavariaceae* (eight in Killerman 1928) are none too satisfactory. Intergrading of some genera makes their limits indeterminate, and lack of information or misunderstanding of structure of others has led to false assumptions. Genera have been set apart variously, but chiefly on differences in form and texture of the basidiocarp; distribution of the hymenium; distinctions of head and stalk regions; presence or absence of sclerotia; and the number of spores borne by the basidia. These lines of segregation fail to separate all genera distinctly. As a result some forms have been shifted to other families and even new families erected to satisfy variations.

For example, Remsberg (1940) has pointed out the confusion existing between *Typhula* and *Pistillaria*, when the distinction between them relies on body form or texture. The presence of a sclerotium in *Typhula* she finds the only good single morphological criterion which is consistently reliable, although the presence of a swollen hymenial portion, the clavula, would seem to be concomitant. Except for this definite character, representatives of

Pistillaria or *Clavaria* might with equal warrant be referred to the genus *Typhula*.

Numbers of spores have not proved good criteria, as witness the claim often advanced that *Pistillaria* basidia are two-spored whereas those of *Typhula* are four-spored (Killerman 1928, Bessey 1935). The fallacy of relying upon such a distinction is clear when one consults Remsberg's work, which showed that two- and four-spored basidia occur freely in typical species of the same genus, and one species is six- or eight-spored. Nor is such variability limited to *Typhula*. Amongst the species of *Physalacria* observed some are consistently two-spored, others are consistently four-spored, and again, in the same species and more particularly in the same basidiocarp, both two- and four-spored basidia occur. Furthermore, in *Clavaria*, defined as a two- or four-spored form, some species have six and eight spores. This would explain Wakyama's statement that the *Clavaria* basidium has eight nuclei; in all probability he had an eight-spored form. No *Clavaria* basidium of the four-spored type has been noted with more than four nuclei.

The question of distribution and position of the hymenium has led to various changes in the family. If only those forms which are distinctly amphigenous are to be regarded as *Clavariaceae*, those genera, of which there are several, whose hymenial distribution is scattered will have to be classified elsewhere. Several such redistributions have been suggested. Krieger (1923), struck by the superficial resemblance of the under lobes of *Physalacria inflata* to the gills of agarics, proposed to move *Physalacria* into a new, transitional family, the *Eoagaricaceae*. Coker (1923) misled by this precipitate judgment, followed Krieger's suggestion and consequently failed to recognize the genus amongst the *Clavariaceae*. McGuire (1939) pointed out that the fertile parts of *Physalacria* were not necessarily on the under side, as Krieger thought, but because they seemed to be unilateral he advocated classifying the genus with the *Thelephoraceae*. Similarly *Sparassis* has been transferred to the *Thelephoraceae* because its hymenium occupies the under sides of the lobes (Cotton 1912), with which assignment Coker (1923) concurs. Sterile lines and areas here and there over the surface of *Clavaria* have long been accepted (Coker 1923), particularly in the forks, though apparently there is no known relationship between the distribution of the hymenium and its position. Clavarias have been found with not only scattered hymenial areas but some blunt projecting cystidial cells. Just as in *Physalacria*, fertile and sterile areas may be recognized by their denser palisade layers. In two species examined these areas were quite distinct, somewhat scattered, and the fertile layer tapered off gradually at the stalk. This returns the question then to the amphigenous nature of the basidiocarp. On that basis *Physalacria* can only be removed if all other forms without completely amphigenous hymenia are removed too.

In the light of the foregoing remarks it would appear that it would be more feasible first to establish limits for the family *Clavariaceae* that are broad enough to include these variations, rather than to scatter too widely those forms which show basic relationships. When more critical knowledge is accumulated for the different genera, re-arrangements and transfers may be in order. For the present any transfer of *Physalacria* from the *Clavariaceae* would seem entirely unnecessary as well as untenable.

In reviewing the published descriptions of already established species of *Physalacria*, a fairly large number is found, thirteen, some of which do not appear to be valid. Of the total only three have been reported from United States. The majority of the remainder are from various parts of the tropics. In addition to previously described forms, specimens collected by G. W. Martin in Panama and Colombia seem to be distinct. Inasmuch as it was impossible to see representatives of all described species, any treatment of the genus as a whole must be tentative. However, since no comprehensive study of the genus exists, descriptions of species seen may prove useful, and a provisional key based in part on publications may serve until such time as more specimens can be critically studied.

KEY TO THE SPECIES

1. Basidiocarps predominantly globular, rugose, hollow ..... 2.
1. Basidiocarps conical, usually small, smooth or rugose, hollow ..... 10.
2. Basidiocarps yellow or pale ochraceous ..... 3.
2. Basidiocarps white or cream colored, often pruinose ..... 4.
3. Spores elongate-elliptical, 13–17 × 2.5–3 μ ..... *P. Clusiae.*
3. Spores oval, 4 × 3 μ ..... *P. stilboidea.*
4. Basidiocarps large, over 1 mm. in diam. ..... 5.
4. Basidiocarps small, under 1 mm. in diam. ..... 7.
5. Basidia typically four-spored ..... *P. inflata.*
5. Basidia two- or four-spored ..... 6.
6. Spores ovoid-elliptical, 6–7 × 3.5–4.5 μ ..... *P. orinocensis.*
6. Spores ovoid to subglobose, 4.5–6.0 × 3–3.5 μ ..... *P. aggregata.*
7. Cystidia lacking, spores roughened ..... *P. Bambusae.*
7. Cystidia present ..... 8.
8. Cystidia conical, flask-shaped, 30 × 8 μ ..... *P. villosa.*
8. Cystidia chiefly ventricose-rostrate ..... 9.
9. Cystidia infrequent, 22–35 × 5–15 μ ..... *P. Langloisii.*
9. Cystidia with conspicuous red-brown resinous heads, 70 × 6–8(–10) μ ..... *P. concinna.*
10. Basidia four-spored ..... *P. Decaryi.*
10. Basidia two-spored ..... 11.
11. Spores 7–10 × 4–5.5 μ ..... *P. andina.*
11. Spores smaller, ovoid-elliptical to pyriform, 3.1–4 × 1.5–2 μ ..... *P. Sanctae-Martae.*

PHYSALACRIA CLUSIAE Syd. Ann. Myc. **28**: 35. 1930. Fig. 76.

Basidiocarps globose, or slightly depressed-globose, the hymenium amphigenous; growing over areas measuring 1.4 cm., clustered or not, ochraceous-yellow; stipes short, 150–220 μ long, 80–140 μ in diam.; hyphae 2–4 μ thick, irregular, rigid and parallel in the stipe; cystidia more or less

prominent, clavate or cylindrical-clavate, 20–50 × 10–20 μ, sometimes possessing an oily-resinous head; cystidia in the stipe short and with a thick covering; basidia clavate, 25–30 μ, sterigmata 2–4(–10) μ long; spores more or less distinctly fusoid, directly or slightly unequal, the apex gradually attenuated, the base abruptly attenuated, possessing a few or numerous minute guttules, continuous, hyaline, 13–17 × 2.5–3 μ.

The only representative of this species seen was so immature that critical characters could not be checked. The description is taken from that of Sydow. Described from Venezuela.

VENEZUELA: Puerto La Cruz, Dec. 30, 1927, Sydow, 760, TYPE (in Farlow Herb.).

PHYSALACRIA STILBOIDEA (Cooke) Sacc. Syll. Fung. **9**: 256. 1891. *Pistillina stilboidea* Cooke, Grev. **19**: 2. 1890.

From the description of this fungus in Saccardo, it appears to be characterized by fleshy, gregarious basidiocarps, pale ochraceous, stipitate, erect, capitate, minute, scarcely 3 mm. high; the head is globose-depressed or globular, hollow, hymeniferous, 0.25–1 mm. in diam.; stipe cylindrical, equal, solid, pruinose, 1.5 mm. long, expanded at the base; basidia cylindrico-clavate, hyaline; spores hyaline, 4 × 3 μ.

Described from New Zealand. No specimens were available for study.

PHYSALACRIA INFLATA (Schw.) Peck, Bull. Torr. Club **9**: 2. 1882. *Mitrula inflata* Schw. in Fries' *Elenchus Fungorum* **1**: 234–235. 1828. *Eoagaricus inflatus* (Schw.) Kr. Md. Acad. Sci. **3**: 8. 1923. Figs. 1–68.

Basidiocarps gregarious, sometimes confluent, or scattered, white, capitate, globose to subglobose, much folded at maturity, hollow, up to a few cm. in diam.; borne on a distinct stalk, centrally or laterally attached, solid, tapering from base to apex, often pruinose from projecting cystidia; hymenium occurring only in restricted areas over the surface of the head, commonly on the side directed downward; cystidia of various form: ventricose-rostrate 26–52 × 4–10 μ, projecting above the surface as much as 30 μ; fusiform cystidia abundant in the sterile areas, less common in the fertile tissue, 40–50 × 4–6 μ, the tip occasionally thickened, projecting up to 50 μ; paraphyses amongst the basidia non-emergent, unencrusted, 27–31 × 2–3 μ; basidia four-spored, 15–18 × 4–5.5 μ; spores hyaline, uninucleate, ovoid-elliptical, 4–6 × 2.5–3.5 μ; growing on dead wood or leaves.

CANADA: Ontario, Aurora, Sept. 25, 1934, *R. F. Cain 3250;* London, Oct. 26, 1889, *Dearness*, ex Ellis Coll., 980 (in Herb. N. Y. Bot. Gard.); Ontario, Magnetwan, Sept. 1921, *L. C. C. Krieger 1310* (in Herb. Univ. Mich.). UNITED STATES—PENNSYLVANIA: Keshan Fall; NEW HAMPSHIRE: Shelburne, June 1888, *Farlow*, ex Ellis Coll.; MARYLAND: Aug. 5, 1891, *Sturgis;* (in Herb. N. Y. Bot. Gard.); WISCONSIN: Door County, Jacksonport, July 25, 27, 1935, *Baker 124;* NEBRASKA: *DeWitt*, June 12, 1938, *J. M. McGuire* (in Herb. Univ. Iowa).

PHYSALACRIA ORINOCENSIS Pat. and Gaill. Bull. Soc. Myc. Fr. **4**: 41. 1888. Figs. 77–82.

Basidiocarps globose, fairly smooth when young, becoming lobed and gyrose with age; white to cream to buff when dry, 0.58–1.6 × 0.55–2 mm., borne on straight or slightly curved, slender stalks, 0.55–0.75(–3.5) mm., sometimes expanded basally, but not projecting far within the head, and terminating there in a few uneven strands; hymenium not amphigenous,

15–24 μ thick; subhymenium scant, rather coarse, about 10 μ thick, resting on a thin layer of reticulate hyphae; cystidia numerous, ventricose-rostrate, often quite large and conspicuously encrusted; smaller fusiform and unencrusted cystidia, not projecting, 12–13 × 3 μ; basidia four- or two-spored, 18–22 × 4–5 μ, sterigmata (2–)3–3.5 μ long; spores ovoid-elliptical, sometimes flattened slightly on one side, laterally apiculate, rarely guttulate, 6–7.5 × 3.5–4.5 μ.

VENEZUELA: July 1887, *Patouillard 81*, TYPE (in Farlow Herb.). PHILIPPINE ISLANDS: Luzon, Mt. Maquiling, Oct. 1920, *Reinking 10034* (in Farlow Herb.). FRENCH INDO-CHINA: Tonkin, Ke So, April 6, 1891, *Bon 4696* (in Farlow Herb.); Hanoi, *Demange 299*, ex Herb. Pat., 1858 (in Farlow Herb.).

Physalacria aggregata Martin and Baker, sp. nov. Figs. 88–93.

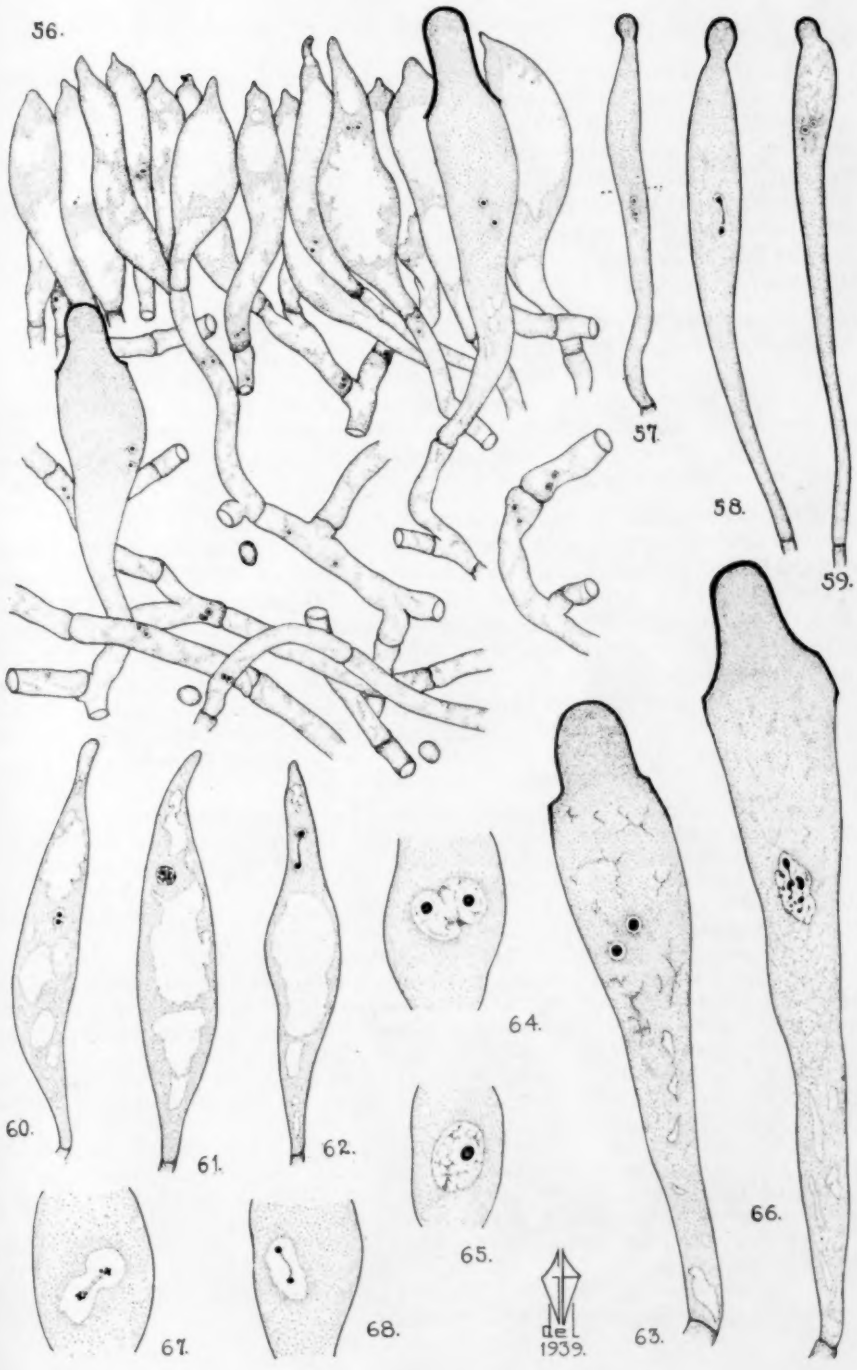
Gregaria vel conferta; capitulum subglobosum vel ellipsoideum, lobatum, cavum, album, sicco ochraceum, 0.5–2.4 × 0.4–1.1 mm.; stipes tenuis, 0.9–1.8 mm. altus; cystidiis duplicibus, ventricosis, rostratis, 50–54 × 9–12 μ, et fusiformibus, incrustatis, 50 × 10 μ; basidiis 4-sporis, raro 2-sporis; basidiosporis ovoideis vel subglobosis, 3.5–6 × 2–3.5 μ.

Basidiocarps more or less spherical, somewhat irregular, lobed, 0.5–1.2–2.4 × 0.4–1.1 mm.; white when young, drying ochraceous; stalks slender, mostly central, 0.9–1.8 mm. high; the head hollow, the stalk projecting slightly into the cavity, ending in a few scattered strands of hyphae; hymenium distributed irregularly over the surface, from 10–15 μ thick, resting on a compact layer about 10–13 μ thick, composed of rather fine, interwoven hyphae; stalk of parallel hyphae which arise from a basal zone of pseudo-parenchyma and terminate in the head in a compact anastomosed mass, not strictly pseudo-parenchymatous as in *P. andina*, finally dissipating in a few strands passing outwards to the margin; cystidia of the ventricose-rostrate type 50–54 × 9–12 μ, originating well below the hymenium and projecting about 8–10 μ; encrusted cystidia 50 × 10 μ; paraphyses in the hymenium 22 × 3 μ; basidia (10–)12–14 × 2.5–4 μ, four-spored, rarely two-spored; sterigmata about 3 μ long; spores ovoid and flattened on one side to subglobose, with a definite lateral apiculus, rarely somewhat reniform (3.5–)4.5–6.0 × (2–)3–3.5 μ.

PANAMA: Chiriquí, Valley of upper Rio Chiriquí Viejo, July 1, 1935, *G. W. Martin 2260, 2261*, TYPE, *2321, 2321a, 2586* (in Herb. Univ. Iowa).

Explanation of figures 56–68.

Physalacria inflata. FIG. 56. Detail of sterile surface cells, including two ventricose-rostrate cystidia. × 1250. FIG. 57. Young fusiform cystidium, pre-fusion, from sterile surface of the head, the surface level marked. × 1250. FIG. 58. Nuclei dividing in a cystidium from the margin of a stalk. × 1250. FIG. 59. Pre-fusion, two-nucleate cystidium from surface of the stalk. × 1250. FIG. 60. Sterile cell from sterile zone with the nuclei fusing. × 2060. FIG. 61. Sterile cell from sterile zone, the post-fusion nucleus dividing. × 2060. FIG. 62. Division of the post-fusion nucleus in a sterile surface cell. × 2060. FIG. 63. Ventricose-rostrate cystidium, two-nucleate, and pre-fusion. × 2060. FIG. 64. Fusion of nuclei in ventricose-rostrate cystidium. × 2060. FIG. 65. Prophase of post-fusion division in ventricose-rostrate cystidium. × 2060. FIG. 66. First division of fusion nucleus of ventricose-rostrate cystidium. × 2060. FIGS. 67, 68. End of the first division in the ventricose-rostrate cystidia. × 2060.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PHYSALACRIA BAMBUSAE von Höhnel, Sitz.-ber. Akad. Wiss. Wien. **118**: 290. 1909.

No material of this species was seen. According to the published description the gregarious basidiocarps are from white to somewhat yellowish when dry, with heads up to 330 μ broad, vesicular, hollow, globular or ovoid, tapering when dry; stipe solid, cylindrical, of thin parallel or irregular hyphae 3–5 μ thick, 360–450 × 40–60 μ; cystidia lacking; basidia 12–14 × 3–4 μ with 4 awl-shaped sterigmata, 5 μ long; spores hyaline, globose, finely roughened, 3–4 μ across; on dead bamboo canes. Described from Java.

The lack of cystidia and the faintly roughened spores should distinguish this species clearly.

PHYSALACRIA VILLOSA Petch, Ann. Roy. Gard. Peradeniya **6**: 206. 1917.

Since no material of this form was available, Petch's account is given in brief. Basidiocarps white, heads globose, up to 0.4 mm. in diam.; stalk up to 0.7 mm. high, tapering from base to apex, 0.1 mm.–40 μ respectively, twisted above, fibrous, rough, with minute crystals and covered with cystidia, 30 × 8 μ, thick-walled, sometimes sub-capitate; basidia four-spored; on dead leaves. From Ceylon.

PHYSALACRIA CONCINNA Syd. Ann. Myc. **28**: 36. 1930.

Basidiocarps solitary or gregarious, white or yellowish-white; stipes very short, 140–180 μ high, 200 μ wide; head globular or subglobose, collapsing in the center when dry, very finely farinose, 350–600 μ diam.; hyphae 1–3 μ thick; cystidia scattered, clavate or cylindrical-clavate, up to 70 μ long, 6–8(–10) μ wide, sometimes capitate, often red-brown, oily, resinous; 12–15 μ in diam.; basidia clavate, 18–22 × 5.1–6.5 μ, 2 or 4 sterigmate; sterigmata 3–5 μ long; smaller cystidia abundant among the basidia, acute, up to 28 μ long; 5–6 μ wide in the mid-region; spores oblique-oval, apex a little attenu-

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Explanation of figures 69–99

Physalacria andina. FIG. 69. Habit sketch of basidiocarps, from *Martin 3489.* × 14. FIG. 70. Longitudinal section, diagrammatic, through a basidiocarp from *Martin 3489.* × 30. FIG. 71. Basidia from type material. × 937. FIG. 72. Spores from the type material. × 937. FIG. 73. Spores from *Martin 3489.* × 937. FIG. 74. Detail of pseudo-parenchyma at top of stalk inside cap of a basidiocarp from *Martin 3489.* × 450. FIG. 75. Cystidia from type material, the surface marked. × 937.

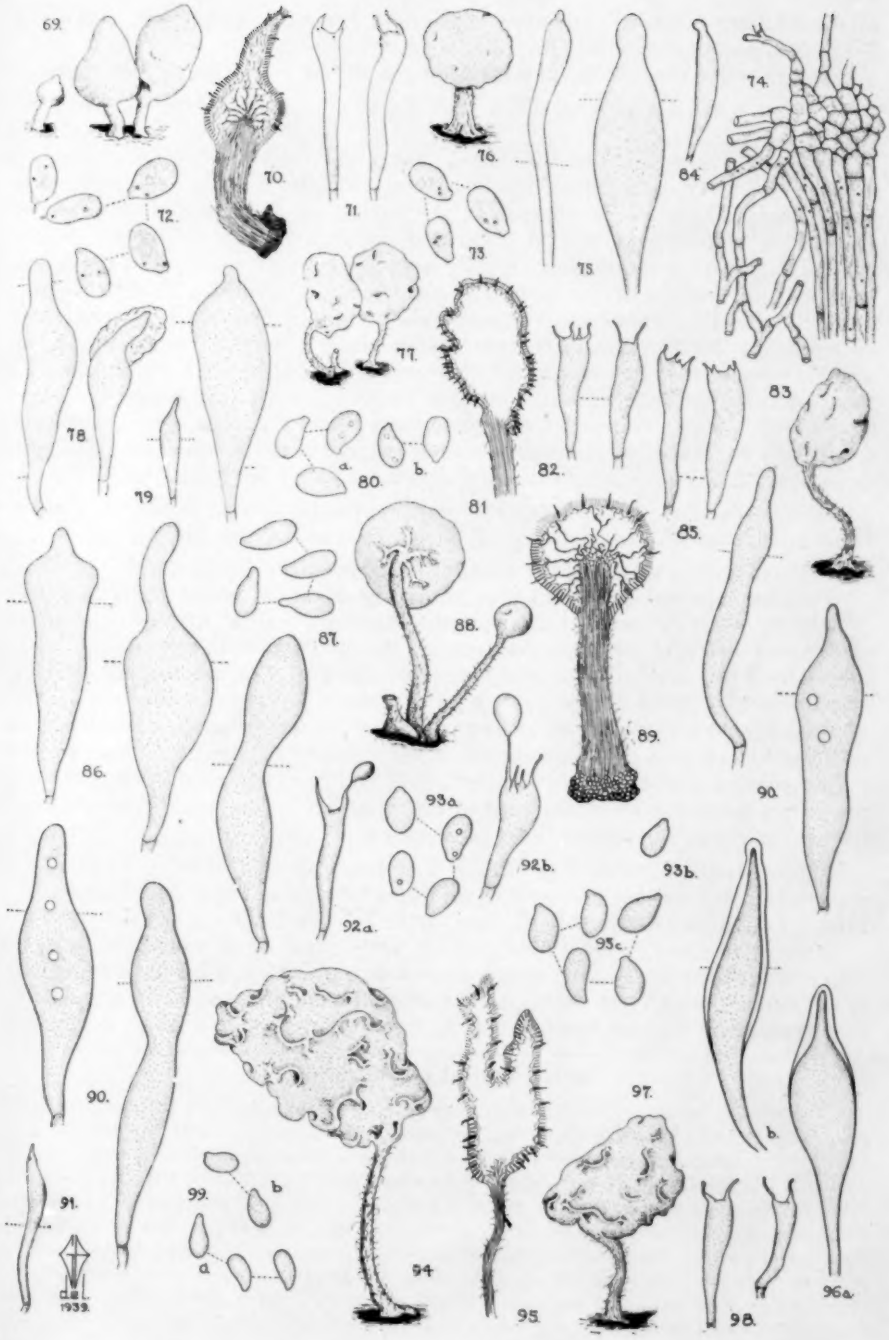
Physalacria Clusiae. FIG. 76. Habit sketch, type material. × 10.

Physalacria orinocensis. FIG. 77. Habit sketch, 4696. × 14. FIG. 78. Three cystidia from 10034 and 4696. × 937. FIG. 79. Paraphysis from hymenium, 4696. × 937. FIG. 80. *a.* Spores from 299. × 937. *b.* Spores from 10034. × 937. FIG. 81. Diagram of internal structure from a section of 10034. × 35. FIG. 82. Basidia, 299. × 1550.

Physalacria Langloisii. FIG. 83. Habit sketch, 91. × 14. FIG. 84. Paraphysis from type. × 1550. FIG. 85. Basidia from type. × 1550. FIG. 86. Cystidia from type. × 1550. FIG. 87. Spores from type. × 1550.

Physalacria aggregata. FIG. 88. Habit sketch, 2261. × 14. FIG. 89. Diagram of section, 2261. × 47. FIG. 90. Cystidia from 2261. × 937. FIG. 91. Paraphysis from hymenium of 2321. × 937. FIG. 92. *a.* Basidium, 2321. × 1550. *b.* Basidia, 2261. × 1550. FIG. 93. *a.* Spores, 2231. × 1550. *b.* Spores, 2260. × 1550. *c.* Spores, 2261. × 1550.

Physalacria Sanctae-Martae. FIG. 94. Habit sketch, 3654. × 14. FIG. 95. Diagram of longitudinal section, 3654. × 14. FIG. 96. *a.* Cystidium, 3485. × 937. *b.* Cystidium, 3654. × 937. FIG. 97. Habit sketch, 3485. × 14. FIG. 98. Basidia, 3654. × 1550. FIG. 99. *a.* Spores, 3654. × 1550. *b.* Spores, 3704. × 1550.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ated, the base rounded, minutely apiculate, apiculus unilateral, 6–8 × 3.0–3.5 μ, continuous, hyaline. Described from Venezuela.

No examples were seen. The foregoing is taken from Sydow's account.

PHYSALACRIA LANGLOISII Ellis and Everhart, Jour. Myc. **4**: 73. 1888. Figs. 83–87.

This species, originally described from the southern United States, is now more widely distributed. Basidiocarps white or slightly yellowish, with heads from subglobose to somewhat attenuated or depressed above, becoming hollow at maturity, 0.25–1 mm. in diam.; stalk fibrous, slightly pubescent, 0.3–1 mm. or more long, usually very long in proportion to the whole basidiocarp; surface of the head not amphigenous; cystidia 22–28 × 5–7.5 μ, projecting 7–13 μ above the surface, (according to Ellis and Everhart the cystidia are 30–33 × 15 μ), clavate, often with a median constriction, or ventricose-rostrate, but never very abundant; paraphyses with the basidia more or less fusiform, 12 × 2 μ; basidia 11–13 × 2.5–3 μ (Ellis and Everhart say 12 × 2.5–3 μ); four-spored, sterigmata short; spores ovoid-elliptical, sometimes flattened on one side, or more rarely a little reniform; apiculus unilateral, 4.2–5 × 1.5–2 μ (Ellis and Everhart say 4.5 × 2–2.5 μ).

UNITED STATES—LOUISIANA: *Langlois*, TYPE, ex Herb. Ellis, (in Farlow Herb.). FLORIDA: Coconut Grove, *Thaxter 91* (in Farlow Herb.).

PHYSALACRIA DECARYI Pat. Mém. Acad. Malgache **6**: 10. 1927.

Basidiocarps entirely white, on decaying wood, in small tufts 3–4 mm. in extent; heads cylindrical, truncated at the top, hollow, attaining a height of 1 mm.; cystidia hyaline, projecting, 25 × 9–10 μ, with an apical beak; spores hyaline, ovoid, 3–4 μ; stipe slender, 150–200 μ thick, bearing cystidia which are 45 × 12–15 μ, also ending in a beak.

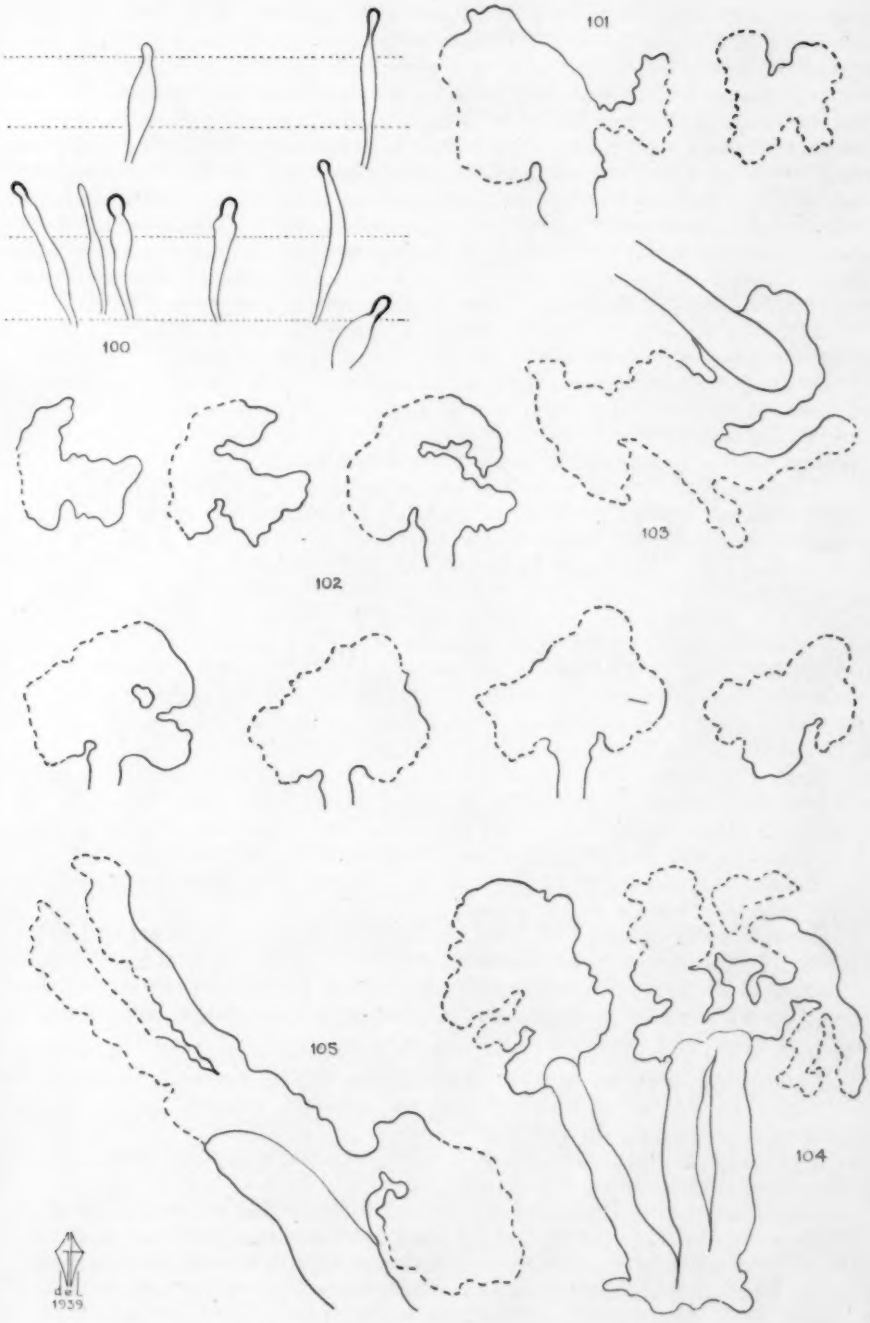
The author's description is drawn upon for the preceding account. In addition he remarks that this species is very closely related to *P. andina* and *P. orinocensis*, but that it is distinguished by its cylindrical form with the truncated summit and by the beaked cystidia. No specimens were obtained for examination. Described from Madagascar.

PHYSALACRIA ANDINA Pat. Essai Taxonomique, 50. 1900. *Physalacria orinocensis* var. *andina* Pat. and G. de Lagerheim, Soc. Myc. Fr. Bull. **9**: 136. 1893. *Physalacria tenera* Syd. Ann. Myc. **28**: 33. 1930. Figs. 69–75.

Two specimens from Patouillard's herbarium were examined, one of which was the type. Examinations were made in a lacto-phenol preparation, in addition to which one basidiocarp was imbedded and sectioned in paraffin. The typical *P. andina* basidiocarp is from definitely conical to acuminate

Explanation of figures 100–105

Physalacria inflata. FIG. 100. Diagrams showing distribution and frequency of large projecting cystidia in sterile (upper) and fertile (lower) surfaces with the surface level and limit of hymenial layer marked with dotted lines. Areas equivalent in extent. × 550. FIG. 101. Diagram of basidiocarp showing hymenial distribution limited to the lower surface. Fertile areas represented by dotted lines. × 15. FIG. 102. Diagram of basidiocarp with irregularly distributed hymenium, at times practically amphigenous in its surface distribution. × 15. FIG. 103. Diagram of basidiocarp showing hymenial distribution on surfaces away from the stalk region. × 15. FIG. 104. Diagrammatic view of three connate basidiocarps with hymenial surfaces on both under and upper sides. × 7.5. FIG. 105. Diagram of basidiocarp with very irregular hymenial distribution. × 15.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from the very beginning and only rarely is the head curved or flexuous, 1–3.5 mm. high, 0.3–2 mm. across; stalk relatively short at maturity, 0.3–0.75 mm.; expanded head 1–2.4 × 0.35–1.2 mm.; surface smooth or slightly rugose, white to deep cream when moistened, appearing decidedly farinose; hollow, but the entire cavity penetrated by sturdy hyphae radiating from the pseudoparenchymatous end of the stipe which extends about 100–300 μ inside the head; stalk hyphae compact, parallel in arrangement, with somewhat thickened walls, binucleate cells; not amphigenous, the surface distinguished by definite fertile and sterile parts; fertile area composed of hymenium, 25–30 μ thick; subhymenium, 15–20 μ thick, poorly defined; and a basal reticulum which connects with the strands from the stalk; cystidia chiefly ventricose-rostrate, 30–40 × 12–15 μ, projecting 15–22 μ above the surface; basidia consistently bispored, (20–)22–24 × 4–5 μ, sterigmata about 3 μ long; spores from ovoid to subglobose with a definite apiculus, binucleate, 7–10 × 4–4.5 μ.

Because of the dried condition of the material when fixed, no satisfactory evidence of nuclear behavior in the basidium could be obtained. Presumably the basidia are four-nucleate and two nuclei move into each spore, for no division figures in the spores were in evidence at all.

P. tenera Syd. is here regarded as the same as *P. andina* Pat. Certainly the material examined gave no justification for maintaining the former as a separate species. The basidiocarps measured 0.75–1.2 mm. × 0.5–0.8 mm., with stalks 0.4–0.75 mm. in height. These measurements are a little under those which Sydow gives (0.75–1.5, rarely 2 mm., with stalks 0.4–1.4 mm.), and both sets of measures are under those of *P. andina*. In section there is no critical difference between them, however. Cystidia range from 40–50 μ and project for 15–25 μ. The basidia, bispored, are 23–29 × 4–4.5 μ (Sydow quotes 20–25 × 5–6 μ); spores 7–10 × 4–5.5 μ; Sydow says 6–11(–12) × 2.5–3.5(–4).

A collection from Colombia, *Martin 3489*, is undoubtedly to be included with the foregoing. The basidiocarps, typically conical, measure 0.8–1.2 × 0.4–0.6 mm., with stalks 0.3–0.5 mm. Their appearance in section is the same as the preceding forms. The basidia, bispored, range from 20 to 22 × 4.5 μ; the spores are bi-nucleate, (5.5–)8–9 × 3.5–4.5 μ. The variations in size amongst these basidiocarps and their basidia and spores is not excessive enough to be significant. The similarity of the internal structure in all three leaves little doubt that they cannot be separated.

ECUADOR: Pululahua, Feb. 1892, *de Lagerheim*, TYPE (in Farlow Herb.); March 1892, *de Lagerheim* (in Farlow Herb.); inter El Limon et Colonia Tovar, Jan. 19, 1928, *H. Sydow 759* (in Farlow Herb.). COLOMBIA—MAGDALENA: Sierra Nevada de Santa Marta, Hacienda Cincinnati, Aug. 18, 1935, *G. W. Martin 3489* (in Herb. Univ. Iowa).

Physalacria Sanctae-Martae Martin and Baker, sp. nov. Figs. 94–99.

Gregaria; capitulum ellipsoideum vel conicum, cavum, album, siccum sature ochraceum; stipes tenuis, 0.8–1.6(–5) mm. altus; cystidiis fusiformibus, parietibus supra crassis, 35–46 × 8–10 μ; basidiis 2-sporis; basidiosporis ovoideis vel piriformibus, 3.1–4 × 1.5–2 μ.

Basidiocarps well developed, ellipsoidal to somewhat conical, pure white, with conspicuous infoldings, 1.4–2.5 × 0.8–1.5 mm., supported by a slender, centrally attached stalk, 0.8–1.6(–5) mm.; pendent; hymenium not amphigenous, 10–15 μ thick; subhymenium slight, about 5 μ, resting on a reticulum 40–45 μ thick; cap entirely hollow, the stalk ending abruptly, in a manner

similar to that of *P. inflata;* cystidia not prominently beaked, tapering markedly, the surface thickened for approximately one-third the length, 35–46 × 8–10 μ, projecting about 12 μ; basidia two-spored with slender sterigmata, 10–12 × 1.5–3 μ; spores small, ovoid-elliptical to pyriform, apiculus lateral, 3.1–4 × 1.5–2 μ.

COLOMBIA—MAGDALENA: Sierra Nevada de Santa Marta, Hacienda Cincinnati, Aug. 18, 1935, *G. W. Martin 3485*, TYPE (in Herb. Univ. Iowa); Cerro Quemado Trail, Aug. 23, 1935, *G. W. Martin 3654, 3704* (in Herb. Univ. Iowa).

SPECIES EXCLUDENDAE

Physalacria rugosa Rick, Broteria **5**: 12. 1906. This species is described as represented by basidiocarps nearly 0.5 mm. in diam., hemispherical, fleshy to somewhat waxy, rugose, stalk pruinose; basidia clavate, 25 μ, sterigmata 3–6 μ long; spores 3.5 × 2 μ, subhyaline; on wood. Described from Brazil.

Lloyd remarks (17) "there has been recently a species (*Physalacria rugosa*) named from Brazil, which I judge from the description is the same as our United States' species."

Two collections of Rick's purporting to be this species were examined but neither proved to be a *Physalacria*. Until authentic material is found it had best be assumed that the species is not a good one.

BRAZIL: Saõ Leopoldo, Rio Grande do Sul, 1929, *Rick;* 1928, *Rick*, ex Herb. F. Theissen, (in Farlow Herb.).

Physalacria solida F. E. and S. E. Clements, Exsicc. Colo. Fungi. The specimen seen did not present typical physalacrian characters, in particular the basidia, which were apparently a heterobasidial type. For this reason it must be excluded from the genus.

UNITED STATES—COLORADO: Minnehaha, Sept. 7, 1906, *F. E. S. S. E. Clements 333* (in Farlow Herb.).

SPECIES DUBIA

Physalacria changensis Rost. in Sacc. Syll. **17**: 203.

The author wishes to acknowledge her indebtedness to the staff of the botany department of Columbia University for placing the full facilities of the department at her disposal during the preparation of this paper, and in particular to Professor J. S. Karling for the reading of the manuscript; to Professor G. W. Martin of the University of Iowa for his tropical collections, the naming of the new species, and his continued counsel; and to the Farlow Herbarium of Harvard University for the use of the library and herbarium.

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POUGHKEEPSIE, NEW YORK

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PAPULASPORA GLADIOLI

B. O. Dodge and Thomas Laskaris

(with two figures)

Much work has been done during the past thirty or forty years on corm diseases of gladiolus. When the complete story is not yet known there is bound to be some confusion regarding those symptoms which can be used to distinguish rots due to particular organisms or agents. Paragraphs with practically identical wording have been published to describe certain phases in corm diseases which were claimed at times to be due to three entirely different fungi. If one compares lists of symptoms given by various authors characterizing scab, heart rot, dry rot, and *Fusarium* rot, he will see the need for a much more careful study of all corm diseases to determine whether the same disease conditions may not be due to different sets of organisms or agents at different times and under different environmental conditions. Not enough attention is given to the work of bulb mites, thrips, and other organisms, which pave the way for invasion by fungi that may be at most only weak parasites, so that one attributes the disease to a certain species at one time and to some other species at another time.

Under the title "The 'smut' disease of *Gladiolus*," the writers (1941a) have pointed out that there is evidence that the fungus which all previous authors, including Wernham (1938) and Zundel (1939) in America, have assumed to be a true smut fungus, *Urocystis Gladioli*, is merely the *Papulaspora* stage of some other fungus, probably an Ascomycete; at least it is not a smut at all. We have found the fungus at various times on about 20 per cent of diseased corms (fig. 1 A) in collections made from a commercial storage house. A core-rot disease caused by a *Sclerotinia* (*Botrytis*) is being further discussed in another paper now in press (1941b). It is true that there is a great similarity between the bulbils of certain species of *Papulaspora* and the spore-balls of a *Urocystis*. Figure 2 B, C, shows two bulbils of the gladiolus fungus.

The method of origin of a spore-ball of *U. Colchici*, as figured by Winter (1876), is much like what one sees in a young culture of our *Papulaspora*. While a few smut fungi have been induced to complete their life cycle, forming chlamydospores in culture, it requires special methods of culture and a long time for the smut to reach maturity. This *Papulaspora* produces its bulbils (fig. 1 B, C) in great numbers within a week's time. Each fertile cell of a *Urocystis* spore-ball theoretically contains two haploid nuclei at first, and these fuse at the maturity of the spore. The central cells of a bulbil of this *Papulaspora* are multinucleate, as is readily shown in cytological preparations. The lighter colored boundary cells also contain three or four, or

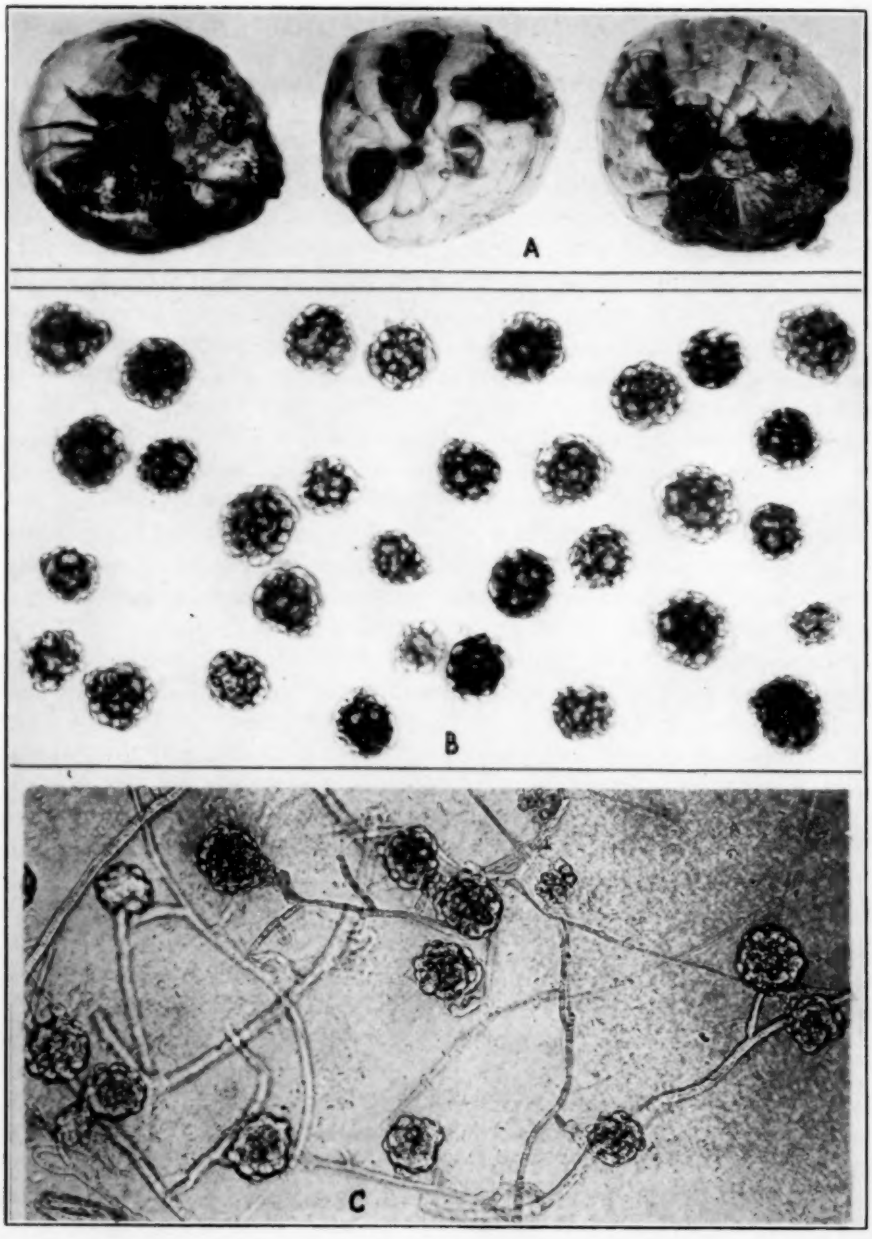

FIG. 1 A. Corms showing types of lesions and mummifications on which mats of mycelium and bulbils of *Papulaspora Gladioli* are formed; B, various types of bulbils; C, bulbils on stalks and characteristic mycelial hyphae.

even more nuclei; the hyphal cells are also multinucleate (fig. 2 E, F). The cytological picture alone would serve to distinguish the bulbils of our *Papulaspora* from the spore-balls of a *Urocystis*. The mycelium is also quite unlike that of a *Urocystis*. It is more like the mycelium of an Ascomycete, such as *Pleurage* or *Ascobolus*. The senior writer (Dodge 1920) proved by single ascospore cultures that *Ascobolus magnificus* has a *Papulaspora* stage (*P. magnifica* Hotson). The bulbils have, as a rule, a single large central cell which is multinucleate, as are the outer pale brown border cells and the cells of the vegetative hyphae. This *Ascobolus* is heterothallic so that races from single ascospores bear only bulbils. When two races of opposite sex are mated, not only bulbils but also ascocarps are developed.

On germinating, smut spores form some sort of a promycelium and the nucleus undergoes reduction. The cells of these bulbils of *Papulaspora* germi-

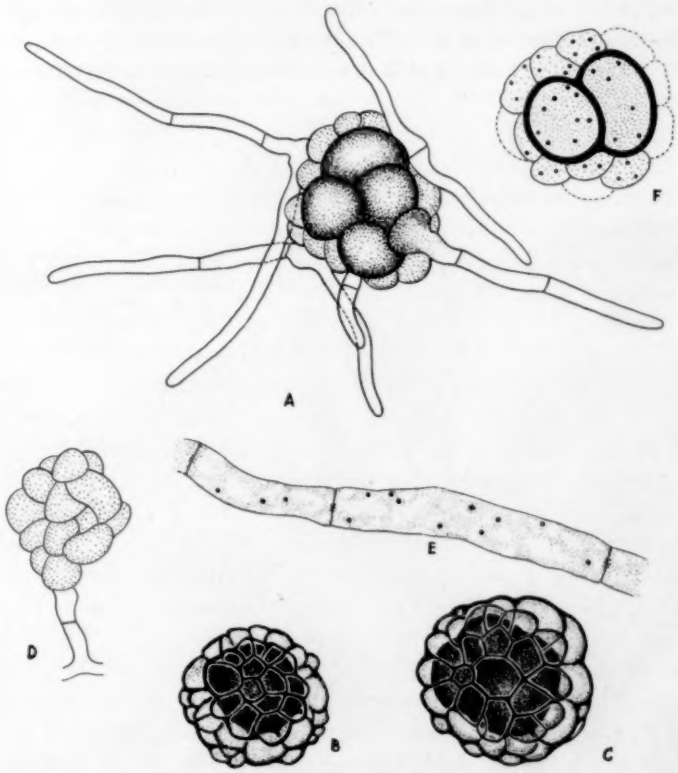

FIG. 2 A. Method of germination of bulbil. The hyaline swollen germ tube basal cell is more or less characteristic, something like the pro-germtube of ascospores of *Neurospora;* B, bulbil with one large central cell; C, bulbil with 3 central cells; D, young bulbil and its stalk; E, multinucleate hyphal cells; F, semidiagrammatic figure showing location of nuclei in a section 5 μ thick of a bulbil. (Drawings by W. L. Graham.)

nate very readily (fig. 2 A) with simple or branching germ tubes, which develop into ordinary hyphae with vacuolate cells and very definite cross-walls upon which there are several deeply staining granules (fig. 2 E). Figure 1 C shows the bulbils borne laterally on stalks.

The fungus grows very readily on manure, decaying fruit and vegetables, and various agar media. Once it becomes established in the soil of a gladiolus planting or in storage houses on debris, it could easily develop whenever conditions were suitable as they are on corms which are diseased or decaying. *Penicillium* certainly aggravates storage troubles. The *Papulaspora* may live mostly as a saprophyte, but also as a very weak parasite, furthering rot or disease primarily due to some other agent.

Smith (1876), who first illustrated spore-balls of *Urocystis Gladioli*, was a real artist. He showed cells of the bulbils readily breaking apart just as they do in spore-balls of *Urocystis*. His illustrations are very diagrammatic, so that the separation of the fertile from the sterile cells may have been idealistic. Brefeld, Magnus, and many noted mycologists have since upheld Smith's conclusions, but it should be remembered that his work on fecundation in *Coprinus* and the formation of oöspores by *Phytophthora infestans* has long since been discredited.

Since there seems to be little question that the fungus heretofore reported as *Urocystis Gladioli* Requien (Smith) is a good *Papulaspora*, we propose to call it *Papulaspora Gladioli* until some one finds the perfect stage. If Requien's type is a leaf smut the combination would simply be *Papulaspora Gladioli* (Smith). *Uredo Gladioli* Requien was described in 1830, so that the specific name will hold if one is guided by common sense and not by the style demanded by the rules of nomenclature prevailing at the moment.

The genus *Papulaspora* was established by Preuss (1851), the type species being *P. sepedonioides*. His colored plate shows the fungus on decaying apple, and mycelial wefts bearing many sporeballs on lateral branches. In general the illustrations would serve very well for *P. Gladioli*, although in detail there are some important differences (fig. 1 B, C). Hotson (1912) adopts the spelling *Papulospora*, but the original spelling by Preuss is *Papulaspora*, which he used on two different occasions the same year.

We have examined specimens of several species of *Papulaspora* in the herbarium of the New York Botanical Garden. Much of this material had been examined by Hotson in former years. Of these *P. rubida* is perhaps most similar to *P. Gladioli*. Specimens identified as *P. sepedonioides* by Sturgis have bulbils which are too small for our fungus. We are not concerned here with listing synonyms, but we wish to include in the emended description measurements of the bulbils and one or two other diagnostic features. The original description of *Uredo Gladioli* by Requien (Duby 1830) is as follows:

"U. Gladioli (Requien in herb. DC.) bifrons, maculis circà luteseentibus,

acervulis nigris suborbicularibus sparsis confertisque convexis epidermide bullata clausa tectis, sporidiis subglobosis sessilibus reticulo pellucido tenuissimo obvolutis—In Gladiolo circa Avenionem (cl. Req.)."

Smith's account (1876) of the fungus on corms is more to the point: "Sori (or clusters of spores in blisters) obliterated or effused, spores large, compound, consisting of from 3 to 6 inner cells and a larger indefinite number of transparent outer cells, both series of cells being fertile. Habitat—On and in corms and scapes of Gladioli." Smith saw mycelia of various fungi and as decomposition progressed the corms were totally destroyed by "diverse fungi, infusoria, nematodes and mites." The "disease" was common in England that year, but he does not say the spore-balls were found on more than the one corm first mentioned.

Our emended description follows:

Papulaspora Gladioli (Requien) Dodge and Laskaris, comb. nov. Mycelium white at first, procumbent, profuse, matted; hyphae septate, cells multinucleate; bulbils on septate stalks, from light to dark brown in mass, spherical, 29–64 μ in diameter with from 1 to 6, occasionally more, central dark brown, multinucleate cells surrounded by a single layer of light brown cortical cells, each with several nuclei. Bulbil primordium a lateral branch ending in a coil. Cells of bulbils germinate with simple or branched germ tubes; in culture bulbils mature quickly, from 4 to 10 days; conidia not seen.

Moore (1939) of England gives the symptoms of the disease in some detail in the paragraph "Smut, Urocystis Gladioli (Req.) (W. G. Sm.)."

"Leaden-coloured, rounded weal-like swellings with yellow margins occur on the corms, stems and leaves of affected plants. Later the skin over these swellings splits, and the dark brown powdery spore masses of the fungus lying below it are exposed. Badly attacked corms may be destroyed and reduced to a blackish-brown powder that consists almost entirely of the spore balls."

This description is clearly a free translation of that given by Pape (1927). Moore includes along with his description a number of references from which it would seem that Van Poeteren (1924–29) at one time carried on experiments for the control of the "smut" disease, which had been troublesome in Holland, especially on the variety Peach Blossom. It was found that by dipping the corms before planting for a period of not more than one half hour in water kept at 110° F. (43.3° C.) the fungus can be killed and the disease controlled. We have immersed cultures of *Papulaspora Gladioli* in water maintained at 44° C. for a half hour. Transplants from the treated culture gave abundant germination of the bulbils within twelve hours. Treating the corms at 43.3° C., therefore, would certainly not be very effective.

Pape (1939) says the sori are also found on leaves and stems. We can not

believe that *Papulaspora Gladioli* would be sufficiently parasitic to attack living green leaves or stems.

SUMMARY

The so-called smut disease on gladiolus heretofore considered to be caused by *Urocystis Gladioli* (Req.) Smith, has been shown to be a species of the form genus *Papulaspora*. The multinucleate condition of the hyphal cells, central and border cells of the bulbil, and the method of germination all clearly indicate that the fungus is not a smut fungus. Neither a fusion nucleus nor a promycelium at germination is evident, and mature spore-balls are formed in culture within a week's time. The bulbils are produced on side branches of a mycelium which grows more or less superficially on diseased corms. Powdery masses of the dark brown bulbils enclosed beneath the scales or in cavities in shrunken diseased tissue simulate sori of *Urocystis* chlamydospores. An emended description is given and a new combination, *Papulaspora Gladioli*, is proposed.

THE NEW YORK BOTANICAL GARDEN
NEW YORK, NEW YORK

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VALIDITY OF EQUATIONS FOR RELATIVE GROWTH CONSTANTS WHEN APPLIED TO SIGMOID GROWTH CURVES[1]

ROBERTSON PRATT

(WITH SEVEN FIGURES)

Huxley (1924, 1932) showed that in many different kinds of organisms the relative magnitudes of parts growing at different absolute rates may be expressed approximately by the equation

$$y = bx^k \tag{1}$$

which may be written

$$\log y = \log b + k \log x \tag{2}$$

where y represents the magnitude of one differentially growing part, x represents the magnitude of the rest of the plant or animal body, or of another part to be compared with the first, b is a constant that indicates the value of y when $x = 1$, and k is a constant that denotes the ratio of the relative growth-rate of the part to the relative growth-rate of the rest of the body, or of the other part.[2] Values of x and y that satisfy this equation locate a straight line when plotted on logarithmic scales.

However, although the formula is a convenient tool and its application to biological data often reveals interesting relations among differentially growing quantities, its use is restricted by definite limitations. This fact was appreciated by Huxley (1932) but seems to have been overlooked by several later investigators who have applied the equation indiscriminately to their experimentally obtained data. The use of this formula has been critically discussed in an earlier theoretical paper (Lumer, 1937).

The purpose of the present report is to emphasize the proposition that double logarithmic plotting of growth data is not a satisfactory substitute for the original data plotted as time curves and that when it is found for any particular set of data that logarithmic plotting according to equation 2 yields approximately a straight line of a certain slope, the parts of the growth cycles for which this applies should be accurately defined because for other parts the slope will be different unless the entire growth cycles coincide.

Huxley (1932) pointed out that the validity of equation 1, as far as its

[1] The ideas presented in this paper are in some measure the outcome of discussions with Professor Sam F. Trelease at Columbia University during the years 1935–1937 and of subsequent discussions with him. His interest in the manuscript is keenly appreciated. The author accepts full responsibility, however, for the validity of the statements made and for the manner of their expression.

[2] Huxley (1932) defined relative growth-rate as the rate of growth per unit weight. Of course it might also be per unit height, volume, or any other measurable quantity.

application to growth data is concerned, rests on the assumption that ". . . since the organ and the body have both existed for the same length of time when we measure them, the time factor cancels out. . . ." It seems of interest to examine this statement with respect to sigmoid curves, since it is this type of curve that is most frequently encountered in studies of the growth of multicellular organisms. It will be shown that even when the organs under consideration "have both existed for the same length of time" when they are measured, the time factor may not always be justifiably cancelled out unless the entire growth cycles are of equal duration.

The curves in figures 1 to 7 show empirically that for organs with sigmoid growth curves, the statement quoted above may be approximately true for portions of the growth cycle; but it should be emphasized that the equation is a precise representation of the facts for the complete period of growth only when the entire growth periods of the quantities under consideration are of equal duration and coincide in absolute time. For a complete picture of the relative growth of two organs (or numbers) the actual measurements and the times at which they were made should be included as the basic experimental data, so that the reader may know just what part of each growth cycle is under consideration, and how the lengths of the entire growth periods compare.

The mathematical analysis and interpretation of sigmoid growth curves is not yet entirely satisfactory, but numerous investigators have shown that the rate of growth of many multicellular organisms and of their parts may be represented approximately by the equation

$$\frac{dx}{dt} = k\,x\,(A - x) \tag{3}$$

Upon integration this becomes

$$\log \frac{x}{A - x} = K\,(t - t_1) \tag{4}$$

which is the equation for the symmetrical sigmoid curve that is characteristic of auto-catalyzed monomolecular reactions. This equation does not always furnish a precise representation of the normal growth curve, but is the simplest expression that affords a reasonably accurate approximation of the sigmoid curves obtained experimentally (Robertson 1908a, 1908b, 1923; Gaines and Nevens 1925; Reed 1920, 1928, 1932; Reed and Holland 1919; Porterfield 1928; Pratt 1936, 1937, 1940; Pratt and Fong 1940; Sideris and Krauss 1938; Albaum, Kaiser, and Eichel 1940). $K = kA/2.3$; x represents the magnitude of the organ or organism at time, t; A denotes the final value of x, and t_1 is the time when $x = A/2$. K is a constant that represents the slope of the straight line that results when values of $\log [x/(A - x)]$ are plotted as ordinates against values of $(t - t_1)$ as abscissas. It is apparent that K is an inverse function of the time required for the growth cycle to reach com-

pletion. Several ideal curves of the form described by equation 4 are drawn in figures 1 and 2.

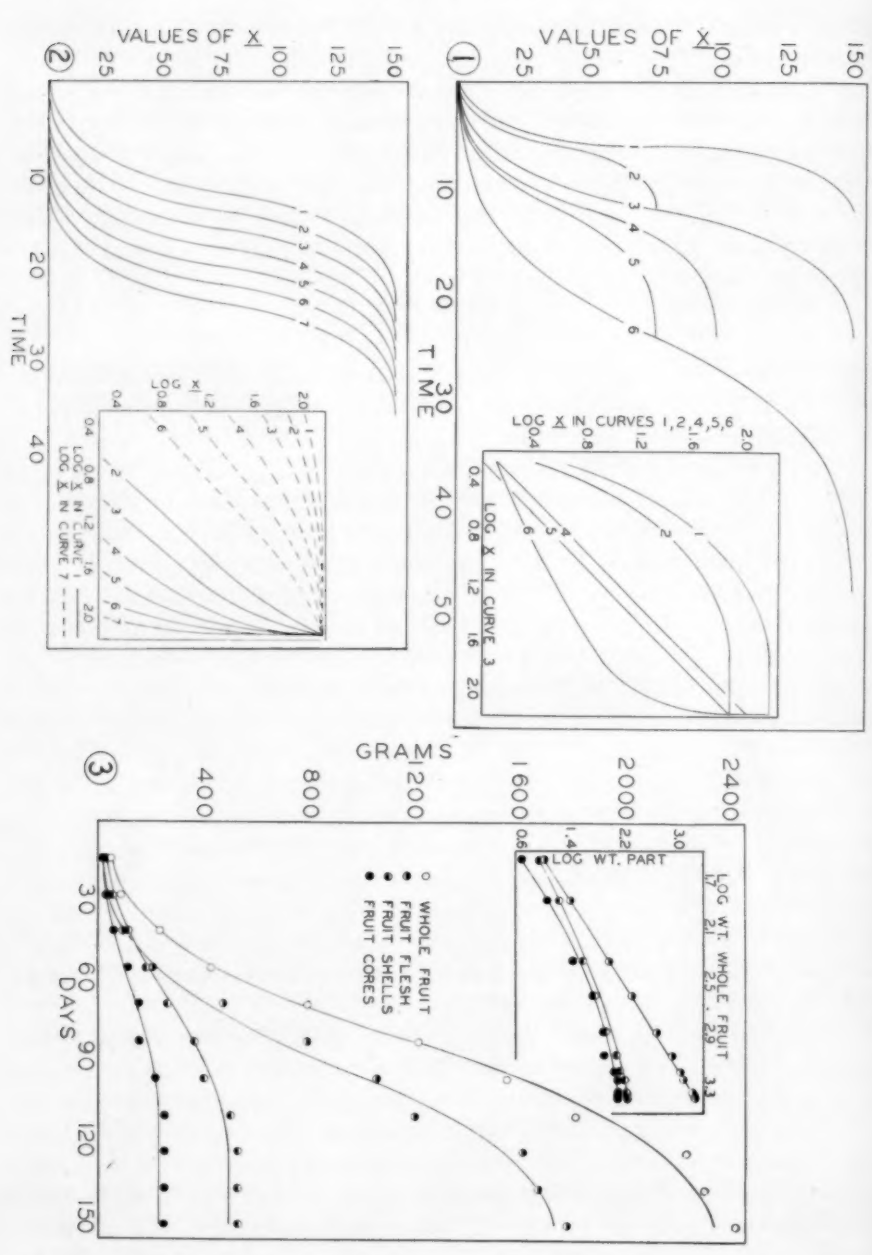
When the growth periods are equal and coincide in time (curves 3, 4, and 5, figure 1), double logarithmic plotting after the manner of Huxley (inset, figure 1) yields a straight line with slope = 1.0. It is clear that the slope can have no other value, since if x and x_1 represent the magnitudes of two quantities, and A and A_1 denote the final values of x and x_1, respectively, then from equation 4 (values of K and t_1 being the same for one curve as for the other) at any time, t

$$\log \frac{x_1}{A_1 - x_1} = \log \frac{x}{A - x} \tag{5}$$

and, therefore, $x_1 \propto x$. Under these conditions, equation 1 becomes simply $y = b\,x$; as the two parts grow, one is always a simple constant multiple of the other.

When the total growth periods are unequal (curves 1, 2, and 6 compared with curve 3 in figure 1) or when they are equal in length but do not coincide in time as, for example, when one organ begins to grow later or ceases growing sooner than another (figure 2), a straight line cannot accurately fit all of the points. The divergence of the curve from a straight line with slope = 1.0 increases as the inequality in length of the growth periods or difference of time increases. The slope of the logarithmic curve approaches, and finally attains, a value of zero as the curve becomes horizontal, or increases without limit as the curve approaches a vertical position. It should be pointed out, however, that even when there is considerable difference in the growth periods, double logarithmic plotting following equation 2 of data from isolated portions of the growth cycles may yield curves that are approximately linear over relatively wide ranges (insets, figures 1 and 2), although the slopes have very different values for the first and last parts of the growth cycles. It is evident, therefore, that when logarithmic plotting gives approximately a straight line of a certain slope, the parts of the growth cycles for which this is true must be defined accurately, since the slope will be different for other parts unless the total growth periods coincide.

Frequently when growth data are plotted according to equation 2, they seem to be fitted best by two straight lines with more or less widely differing slopes, and several investigators have attempted to ascribe biological significance to the break that occurs in these curves. When the original data are not given as time curves or in tables, it is difficult for the reader to evaluate such conclusions. It should be pointed out, however, that several of the curves in the insets of figures 1 and 2 might, if based on biological data which generally show greater or less variation, be easily thought to represent two straight lines with different slopes. It is apparent, therefore, that such a curve does not necessarily indicate any pronounced change in the metabolism


VALUES OF X
TIME
LOG X IN CURVES 1,2,4,5,6
LOG X IN CURVE 3
LOG X IN CURVE 1 ——— 2.0
LOG X IN CURVE 7 - - - -
GRAMS
DAYS
WHOLE FRUIT
FRUIT FLESH
FRUIT SHELLS
FRUIT CORES
LOG WT. PART
LOG WT. WHOLE FRUIT

or physiological activity of the organs but may be merely the inevitable result of comparing two quantities whose periods of increment are not entirely concurrent.

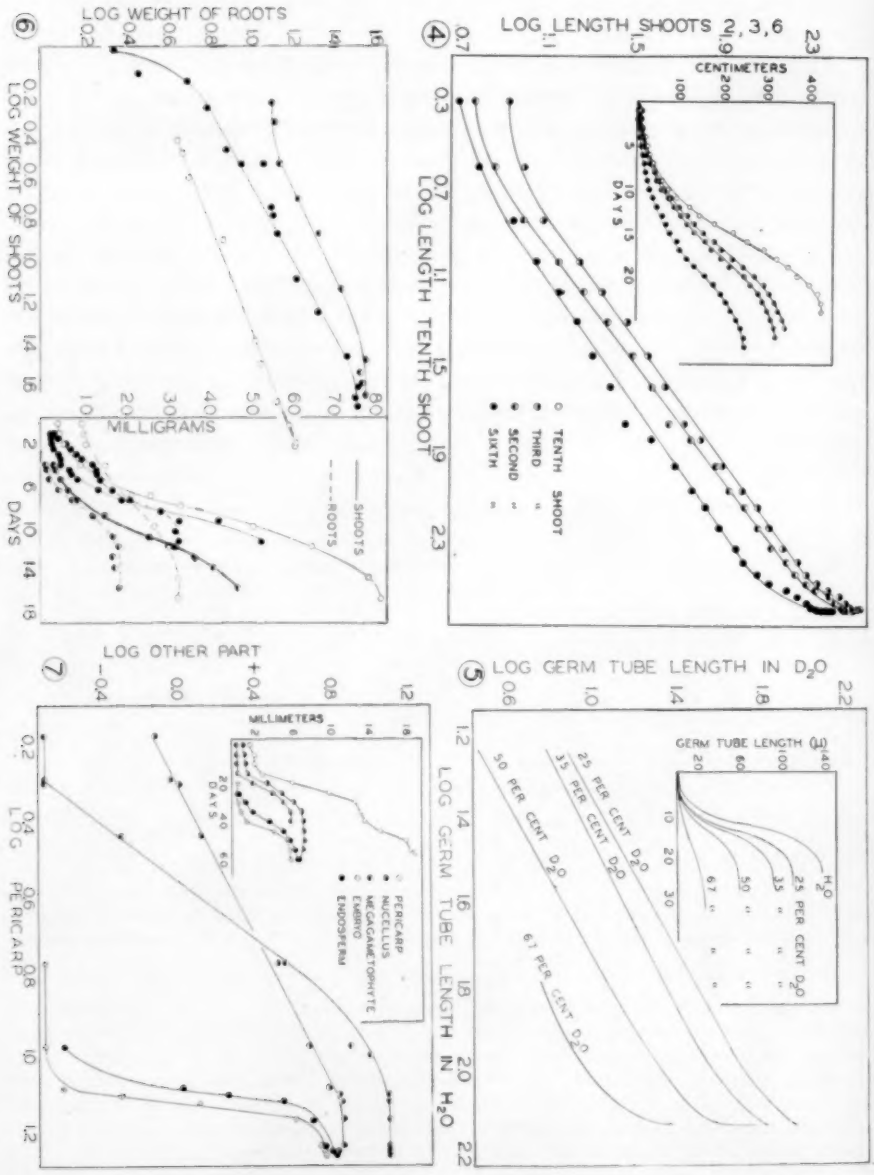
The relations discussed above are not peculiarities of "ideal" sigmoid curves. This is shown by figures 3–7 and table 1 where experimentally obtained data are presented. The integrated growth curves are all of the sigmoid type, those of Porterfield, of Pratt, and of Sideris and Krauss being reasonably accurately described by an equation with the general form of equation 4 or a simple modification of it.

It should be noted that in all cases where the growth periods do not coincide the slopes of the logarithmic curves vary from finite values to infinity or zero, although the logarithmic plots seem to be approximately linear for certain discrete portions of the curves considered separately. The departure from a straight line increases with the disparity of the total growth periods; but when different quantities increase in a sigmoid manner through approximately the same period of time, double logarithmic plotting yields

FIG. 1. Curves drawn according to the equation $\log \frac{x}{A-x} = K(t-t_1)$ where x (ordinate) represents the magnitude of the quantity under consideration at any time, t; A denotes the final value of x, and t_1 is the time when $x = A/2$. K is a constant that varies inversely with the time required for the growth cycle to reach completion. The different curves have the following constants:

	A	K	$2t_1$ = full length of growth period
Curve 1	150	0.374	12
" 2	75	0.374	12
" 3	150	0.187	24
" 4	98	0.187	24
" 5	75	0.187	24
" 6	150	0.094	48

Inset: Logarithms of values of x in curves 1, 2, 4, 5, and 6 plotted as ordinates against logarithms of values of x in curve 3 at corresponding times. FIG. 2. Curves drawn according to the equation $\log \frac{x}{A-x} = K(t-t_1)$. In each curve, $A = 150$, $K = 0.187$, and the total growth period = 24. Each curve is separated from the next one by two units on the abscissa, so that although all the curves increase for the same length of time the growth periods do not coincide. *Inset:* Solid lines show logarithms of x from curves 2, 3, 4, 5, 6, and 7 (ordinates) as functions of log x in curve 1 at corresponding times. Discontinuous lines show log x from curve 7 on the abscissa scale and log x from the other curves on the ordinate. FIG. 3. Growth of whole fruits and of their parts in the pineapple (*Ananas sativus*). *Inset:* Logarithmic plotting to show the relative growth of the parts compared with the whole fruit. The integrated curves are drawn according to the equation $\log \frac{x+a}{A-x} = \log \frac{a}{A} + Kt$ where x, A, K, and t have the same significance as in equation 4 and where a represents the value of x when $t = 0$. The points indicate experimental observations. The data were taken from Sideris and Krauss (1938).


6
LOG WEIGHT OF ROOTS
LOG WEIGHT OF SHOOTS
MILLIGRAMS
DAYS
SHOOTS
ROOTS
4
LOG LENGTH SHOOTS 2, 3, 6
LOG LENGTH TENTH SHOOT
CENTIMETERS
DAYS
TENTH SHOOT
THIRD "
SECOND "
SIXTH "
5
LOG GERM TUBE LENGTH IN D2O
LOG GERM TUBE LENGTH IN H2O
GERM TUBE LENGTH (μ)
50 PER CENT D2O
35 PER CENT D2O
25 PER CENT D2O
61 PER CENT D2O
H2O
7
LOG OTHER PART
LOG PERICARP
MILLIMETERS
DAYS
PERICARP
NUCELLUS
MEGAGAMETOPHYTE
EMBRYO
ENDOSPERM

straight lines for the entire growth periods and k values are approximately 1.0 (table 1). Thus it may be seen that the empirical observations are in agreement with expectations based on theory.

It is of interest now to examine some of the data on "chemical heterogony." Numerous investigators have studied the chemical composition of animals at different stages of development and some have employed the Huxley formula to describe the relative abundance of chemical constituents in the organisms, or their parts, at different times. Needham (1934) summarized and reviewed many sets of these data. Seventeen substances and twenty-six species of animals ranging from Crustacea to mammals were considered, and it was found that in nearly every case a straight line resulted when the logarithm of the magnitude of the chemical entity at any time was plotted against that of the chemical totality, i.e., dry or wet weight, at the same time.

A portion of Needham's paper is devoted to speculation concerning the "general significance" of the fact that "... organisms of extremely different morphological form give identical differential growth ratios for a given chemical substance" and it was suggested that "genetic differences and interphyletic differences occur only at a supra-chemical level."

It should be observed, however, that not only were the differential growth ratios "identical" for a given chemical substance, but that they were essentially the same for most of the substances studied, i.e., about 1.0. Most of the

FIG. 4. Logarithmic plots to show the relative growth rates of different shoots of bamboo, *Phyllostachys nigra*. *Inset:* Original data plotted arithmetically. The data were taken from Porterfield (1928). FIG. 5. Logarithms of *Erysiphe* germ tube lengths in different concentrations of heavy water (ordinates) as functions of logarithms of germ tube lengths in ordinary water at corresponding times. *Inset:* Original data plotted arithmetically. The curves are drawn according to the equation $\log \frac{x}{A-x} = K(t-t_1)$ and have the following constants:

	A	K	$2t_1$ = full length of growth period
H_2O	136.8	0.187	24.76
25 per cent D_2O	110.7	0.183	27.50
35 " " "	91.0	0.165	27.26
50 " " "	59.4	0.174	28.00
67 " " "	24.5	0.127	32.50

The data were taken from Pratt (1936) and from unpublished material.

FIG. 6. *Left:* Logarithmic plots to show the relative growth-rates of roots and shoots in different lots of peas (*Pisum sativum*). *Right:* Arithmetic plots of original data. The data were taken from Pearsall (1923). FIG. 7. Logarithmic plots to show the relative growth rates of different parts of the fruit in an early-ripening variety (Early Purple Guigne) of sweet cherry, *Prunus avium*. Curves labelled nucellus and megagametophyte, respectively are for nucellus + integuments and for megagametophyte + embryo sac. *Inset:* Original data plotted arithmetically. The data were taken from Tukey (1933).

sets of data analyzed by Needham pertain only to the early stages of growth when the rates of increase were rising, but it seems reasonable to assume that had data for the entire life of each of the different organisms been plotted, sigmoid curves would have resulted. It may also be reasonable to assume that in a given organism, permitted to grow to maturity, the different substances ("chemical entities") studied would have increased through approximately the same period of time as the dry or wet weight ("chemical totality"), i.e., as long as the organism continued to grow. Hence, heterogonic plots based on theoretically ideal data for each organism would have yielded straight lines with slope = 1.0. The mean value of k calculated from sixty-nine published observations (Needham 1934) is 1.1 ± 0.02. This is remarkably close to the expected value of 1.0, when allowance is made for the normal variation of living organisms, the diverse conditions under which the data were obtained, and the fact that the value of k in each case depends largely upon the statistical accuracy of each of the individual sets of data on which it is based. It seems, therefore, from the discussion presented above that perhaps one should not be too prone to attach special significance to the "uniformity of chemical heterogony in widely different organisms."

As similar examples from the botanical literature, the studies of Gaines and Nevens (1925) and of Bisson and Jones (1932) on the chemical composition of sunflower and pea crops respectively have been selected. The data have been plotted after the manner of Huxley and the k values calculated. The average values of k for the total carbohydrate and total nitrogen (substances for which the data seem most reliable) are 0.99 and 0.96 respectively. These values of k and those for the different mineral components which also increased during approximately the same period of time as the dry weight

TABLE 1

Components of pea and sunflower plants as functions of dry weight[1]

Component of plant	Plant	Investigator	k = relative growth constant
Total carbohydrate	Pea seeds	Bisson and Jones	0.98
" "	Sunflower seeds	Gaines and Nevens	0.97
" "	" crops	" " "	1.02
" ash	Pea seeds	Bisson and Jones	0.95
" "	Sunflower seeds	Gaines and Nevens	0.83
" "	" crops	" " "	0.84
" nitrogen	Pea seeds	Bisson and Jones	0.92
" "	Sunflower seeds	Gaines and Nevens	0.99
" potassium	Sunflower seeds	" " "	0.94
" sulphur	" "	" " "	0.99
" magnesium	" "	" " "	1.02
" calcium	" "	" " "	0.72
" phosphorus	" "	" " "	0.84
		Av. value of k =	0.92

[1] The periods of increment of the different components listed and of the dry weight, with which they were compared, were nearly coincident in all of the plants listed.

are shown in table 1. The mean value of k is 0.92, a figure remarkably close to the expected value of 1.0.

It should be emphasized that the remarks made in this paper pertain specifically to sigmoid growth curves. Many other kinds of growth curves will give straight lines when plotted according to Huxley's formula. When this is so, it means merely that the slope of one original semi-logarithmic curve (log size against time) is always a constant multiple of the slope of the other. The constant factor by which the two slopes differ represents the slope, or k value, of the Huxley line. If the original semi-logarithmic curves have the same slopes during the same time intervals, the Huxley k is 1.0.

SUMMARY

Application of the Huxley equation $y = bx^k$ to growth data in order to express the relative growth-rates of different organs often reveals interesting relations among differentially growing quantities. Its use is restricted by definite limitations, however.

When the equation is found to fit the observed data, the parts of the growth cycles to which it applies should be accurately defined, because for other parts the slope of the logarithmic curve (k value or "relative-growth constant") may be quite different.

Logarithmic plotting of growth data in accordance with the Huxley formula is not a satisfactory substitute for the original data plotted as time curves.

If the growth cycles of the two quantities coincide in time and follow the sigmoid course of the curve for an autocatalytic monomolecular reaction that is characteristic of the growth of many multicellular organs and organisms, the k value, or relative growth constant, as determined by the Huxley equation, is 1.0. The value of y then remains a simple multiple of x; i.e., $y = bx$.

When the total growth periods are unequal or when they are equal but do not coincide in time, a straight line cannot accurately fit all of the points, although isolated portions of the growth cycles may yield curves that are approximately linear over relatively wide ranges. The slopes may have very different values for the first and last parts of the growth cycles, however, approaching a value of zero as the curve becomes horizontal, or increasing without limit as the curve approaches a vertical position.

A sharp break in the relative-growth curves does not necessarily indicate a fundamental physiological change in the organism as some investigators have suggested, but may be merely the inevitable consequence of comparing two quantities whose periods of increment are not entirely concurrent.

The remarks in the present paper refer specifically to relative-growth constants of quantities that increase as sigmoid functions of time. They are not intended to apply to other types of growth curves, although it is possible they could be extended to cover other cases also.

The statements and conclusions of the present paper are supported empirically by "ideal" curves calculated from equations commonly employed in growth studies and by curves constructed from data in the literature.

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THE INFLORESCENCE IN HEMEROCALLIS—I

A. B. STOUT

(WITH TWENTY-TWO FIGURES)[1]

THE ORIGIN OF THE SCAPE

In *Hemerocallis* the plant is an herbaceous perennial and the numerous, short, somewhat thickened, and much intertwined branches in the crown of the plant bear coarse, grass-like, and closely equitant leaves in two ranks which rise from a crown-branch into the air as "fans." A flower scape arises from a leafy stem in the crown and is terminal for the axis immediately below it.

When a scape is located in the center and apex of a fan of leaves its terminal position is evident. It stands between the concave and upper surfaces of the two leaves which arise from the two nodes which are immediately below the scape and of the same axis; and vegetative laterals are lacking in the axils of either of these leaves. The relation of the axis and the two leaves is as shown in figure 1 for the leaves labeled *L2* and *L3*.

Frequently a scape appears to be a lateral on the stem of a single fan of leaves. But in such cases the vegetative shoot that appears to rise above the base of the scape is the real lateral that arises in the axil of one of the uppermost leaves of the main axis that continues into the scape. Figure 1 shows the relationships when the vegetative shoot is in the axil of the uppermost leaf (fig. 1, *L3*) that clasps the base of the first internode of the scape. When but one vegetative lateral develops and is located in the axil of the next to the last leaf, the scape also stands between two equitant leaves but now the leaf that clasps the base of the scape has no axillary branch.

A scape may stand between two vegetative branches (see fig. 2), in which case the main axis that continues into the scape has two laterals; one may arise in the axil of the leaf that clasps the base of the first internode (*L3* of fig. 2) of the scape and one is in the axil of the next leaf below (*L2* of fig. 2). These two branches are on opposite sides of the scape which now stands between the convex surfaces of two leaves (*L3–1* and *L4–1* of fig. 2) each of which belongs to a different lateral. During a single period of flowering two scapes may arise as successive terminals in a single fan of leaves.

In the formation of a scape, its first segment or internode is greatly modified, especially in respect to elongation and to reduction in diameter, in contrast to the internodes immediately below it and to those of any lateral in the crown (compare internode *4* with *3* and *4–1* in fig. 1). When a

[1] Assistance in the preparation of the figures of this article was furnished by the personnel of the Works Progress Administration (O.P. 165–1–97–8. W. P. 5).

scape appears to be a lateral it is the vigorous vegetative growth of its own basal lateral as a leafy crown-branch that continues the two ranks of leaves in such a manner that the shift from terminal to a lateral is not obvious to casual observation. But the arrangement of the leaves about the base of the scapes clearly indicates that a scape is terminal on the axis immediately below it.

THE SIMPLE INFLORESCENCE OF H. NANA

In the species *Hemerocallis nana* the flowers are solitary and terminal for the main axis of the scape and for each of the few laterals which develop on the scape. There are no traces in the axils of the bracteoles of the laterals which, in all other species now recognized, form the bostryxes of the inflorescence.

The one-flowered scapes. Frequently the normally developed scapes on plants of *H. nana* bear a solitary flower below which there are two modified leaves (fig. 3). These are placed not far below the flower and the upper and smaller one (a bracteole) is often clearly placed on the axis at an angle that is approximately 90° from the position of the lower one (a bract).

The distribution of vascular bundles in a typical single-flowered scape

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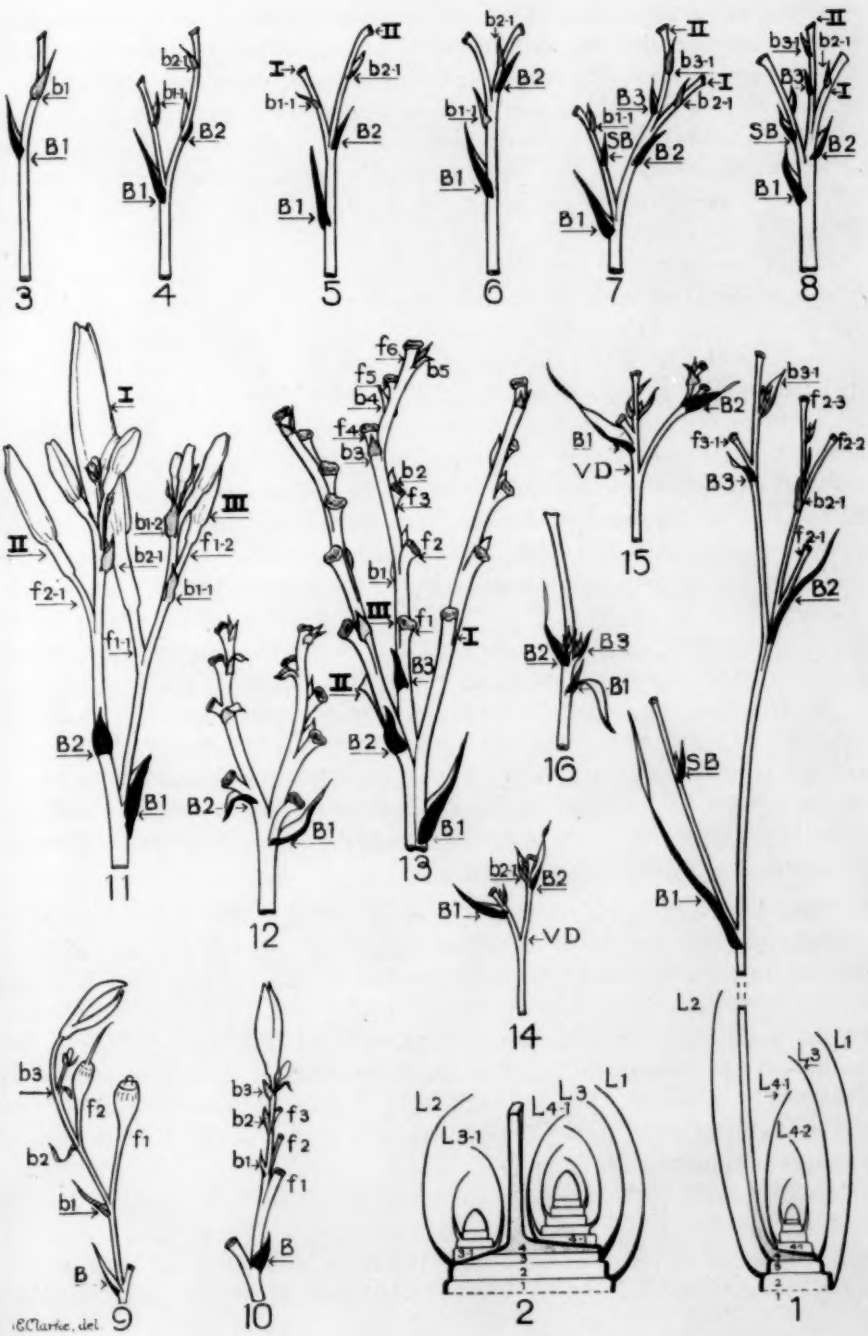
Explanation of figures 1–16

All figures except 1, 2, 9, and 10 are approximately one-half natural size. In most cases the drawings were made for scapes that had ended flowering. Most capsules and flowers, if present, were omitted and the ends of pedicels shown as when the flowers abscise below the ovary. In the lettering the designations are as follows: *L*, leaves of crown branches; *B*, bracts on the main axis of a scape; *SB*, bracts on lateral branch; *VD*, vegetative dichotomy of which both arms continue as an internode until there is a bract; *b*, bracteole, also not so heavily shaded as bracts; *f*, flower; Roman numerals (I, II, III) indicate succession in development and blooming.

FIG. 1. Lower portion is diagram of section showing relations and positions of parts when a scape has a vegetative crown lateral that is axillary to the leaf (*L3*) that is located at the base of the first internode of the scape. Upper portion shows a scape of *Hemerocallis minor* with a primary inflorescence of two bostryxes, below which there is a lateral branch bearing only one flower. FIG. 2. Diagram of sectional view of a scape which has a vegetative crown lateral in the axil of each of the two uppermost leaves (*L2* and *L3*) of its crown axis. FIGS. 3–8 inclusive. Scapes of *Hemerocallis nana*. FIG. 9. Nondichotomous bostryx of *Alstroemeria revoluta*. Copied from illustration by A. and L. Bravais. FIG. 10. Dichotomous bostryx of *Hemerocallis fulva* clone Europa. Copied from illustration by A. and L. Bravais. FIG. 11. A two-bostryx primary inflorescence of the Europa daylily at the time when the first flower is ready to open. FIG. 12. A two-bostryx primary inflorescence of the Europa daylily after all flowers have bloomed and fallen. FIG. 13. A three-bostryx primary inflorescence of the Europa daylily. FIGS. 14, 15. Upper portion of scapes of *H. minor* showing vegetative dichotomy in the first internode of a scape. In figure 14 each bostryx is reduced to one flower; in figure 15 each is reduced to two flowers. FIG. 16. Scape of *H. minor* bearing one flower which is terminal on the lateral belonging in the axil of bract 2. The dichotomous lateral to the pedicel of this flower, the lateral in the bract below, and the terminal of the main axis above bract 3 are all aborted.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was studied in cross-sections at levels below the bract and the bracteole, midway between the two, and above the bracteole. In the upper portion of the first internode of the scape, in a cross-section, there was a central core of pith cells about which there was a zone of cells that had thick walls (stereome tissue). Rather evenly distributed throughout the stereome there were numerous (about 35) fibrovascular bundles. In the segment of the stereome directly below the bract (as *B1* of fig. 3) the vascular bundles branched and supplied veins to the bract but no bud was organized in its axil and the main axis continued as a single stem. Immediately below the bracteole (as *b1* of fig. 3) branches of bundles in the stereome supplied veins for the bracteole but no lateral was organized and no abortion of one was present. At this level and above in the pedicel the stereome was less defined and the bundles were more equally distributed within the scape.

It seems certain that in this species the main axis of a single-flowered scape continues as a single stem throughout its first internode, through the segment between the bract and the bracteole and on into the pedicel of the flower. But the character of this axis does change: the first internode is relatively long, as much as twelve or more inches in this dwarf species, while the second internode, or peduncle, is very much shorter; the phyllotaxy changes from the two-ranked and 180° spacing to one of only 90°; in the internal structure there are a decrease of the stereome and a more central distribution of vascular bundles, especially in a pedicel.

In *H. nana* the flower of a normal single-flowered scape is obviously terminal. For the purposes of this discussion it will be considered that such a scape is differentiated into (1) a long internode which terminates at the primary bract (*B1* in fig. 3), (2) a peduncle of one internode which terminates at the bracteole (*b1* in fig. 3), and (3) a pedicel that terminates in a flower.

Two-flowered scapes (figs. 4, 5, and 6) are frequent among plants of *H. nana* and they may occur on the same plant with scapes that bear solitary flowers. In these the lower flower is the first to open, and it (fig. 4) is the terminal of a lateral that arises in the axil of the lower of two primary bracts on the main stem. In such a lateral there is an internode (which is the peduncle) and a bracteole (*b1–1* in fig. 4) above which the axis continues as a pedicel of a flower. Thus the main axis of a two-flowered scape has two internodes. The lower flower is terminal on a lateral branch and the upper flower is terminal on the main axis.

The lateral branch dominates the main axis above it in vigor of growth and in time of maturity. Often its organization as a separate axis is delayed and it is more or less combined with the main axis until the level of the second bract is reached (fig. 5). The bracteole that belongs on the lateral may

even be placed (fig. 6) below the level of the complete separation of the lateral.

Three-flowered scapes. Drawings of typical three-flowered scapes from plants of *H. nana* are shown in figures 7 and 8. The two apical flowers are like those of the two-flowered scapes. Below these the main axis has an additional internode and a primary bract in the axil of which there is a lateral. In such scapes the lower of the two laterals often has an internode, a secondary bract, a peduncle, a bracteole, and a pedicel that ends in a solitary flower (figs. 7 and 8). Frequently there is delayed separation of the lower lateral (fig. 8).

All the three-flowered scapes seen by the writer were on plants that were growing in the Royal Botanic Garden at Edinburgh, Scotland, and which were at the time through blooming. When the lower lateral of a three-flowered scape of *H. nana* has a vegetative internode and a secondary bract, it seems that its flower opens later than does the flower on the lateral which is above it (figs. 7 and 8).

Irregularities in the development of scapes in plants considered to be *H. nana* have been noted. Scapes with solitary flowers have been observed which had as many as four bracts in the axils of which there were no signs of any lateral. In others there were scapes in which the main axis above the second bract was more or less undeveloped and in some cases reduced to a mere stub. The irregular and delayed separation of laterals may be such that there is the interpolation of two or more axes at one level with the placing of bracts and bracteoles at irregular positions. These features of growth are more conspicuously developed in other species of the genus in which the entire inflorescence is much compacted.

A comparison of scapes of *H. nana* which bear one flower, two flowers, and three flowers shows that the uppermost flower is terminal on the main axis and is alike in all three. The two-flowered scape has in its main axis one additional internode with a lateral to its bract. The three-flowered scape has still another internode with a bract and a lateral. Thus the additional flowers are produced by an increase in the number of internodes in the main axis and the formation of laterals.

In the species *H. nana*, as far as the writer observed, there are no indications of secondary laterals, either rudimentary or otherwise, which arise in the axil of any bracteole. In the three-flowered scape both the terminal and the lateral immediately below it have each only a peduncle and a pedicel and the two combine to form what may be called a terminal inflorescence. When a lateral below these two has an extra internode and bract and is later in the maturity of its first flower it may be considered as a secondary inflorescence.

Not only does the species *H. nana* have the simplest inflorescence of any

of the known and recognized species of *Hemerocallis*[2] but it is the smallest in stature and it has, according to present knowledge, a very restricted distribution in the interior of China.

THE NATURE OF THE BOSTRYX

It now appears that, except for *H. nana*, the "dichotomous" bostryx is present in all species of *Hemerocallis*. Also two or more bostryxes combine to form a primary inflorescence that is terminal for the entire scape. In much-branched species the laterals below such an inflorescence have one or more secondary bracts above which the bostryxes form secondary inflorescences.

The nature and character of the dichotomous bostryx in *Hemerocallis* will be more readily understood if there is first a consideration of the unforked bostryx in other genera.

The nondichotomous bostryx was recognized and described as a "Schraubel" and as a "Bostryx" as early as 1835 (Schimper according to Braun 1835). Soon thereafter (1837), L. and A. Bravais designated this type of branch a "cime uninodale helicoide" and these authors made a somewhat comprehensive survey of its occurrence and modifications in the inflorescences of flowering plants. They noted that the helicoid cyme in flowering plants may be elongated or shortened, axillary or terminal, *single or dichotomous*, and that bracteoles may fail to develop, or they may be present in normal position at the base of a pedicel, or they may be transposed to other positions.

The simple (nondichotomous) bostryx or uninodal helicoid cyme was illustrated by L. and A. Bravais in the species *Alstroemeria revoluta* and their figure is here reproduced (fig. 9). In this, the first flower in a series of flowers is terminal on the axis immediately below it. In this axis there is a peduncle with one node ("uninodale") at which there is a bracteole; above the bracteole there is one pedicel which ends in a flower. But a lateral to this pedicel develops in the axil of its bracteole and continues to form a new peduncle which terminates above its own bracteole in a pedicel and its single flower. The relation of flower pedicel to its lateral is continued to form the successive flowers above until there is an abortion of the new lateral. The successive peduncles combine to form a false axis. There is but one row each of bracteoles, of units of the false axis, and of pedicels and flowers, and these are arranged in an ascending spiral which continues in one direction. It is this single, ascending, spiral arrangement with the decreasing size of the flowers, bracts, and stem units that suggested the terms "helicoid" (like a snail shell), "schraubel" (a screw), and "bostryx" (a curl). In contrast

[2] At present the writer does not consider that the description and herbarium material of the so-called *H. plicata* are adequate for the designation of a distinct species.

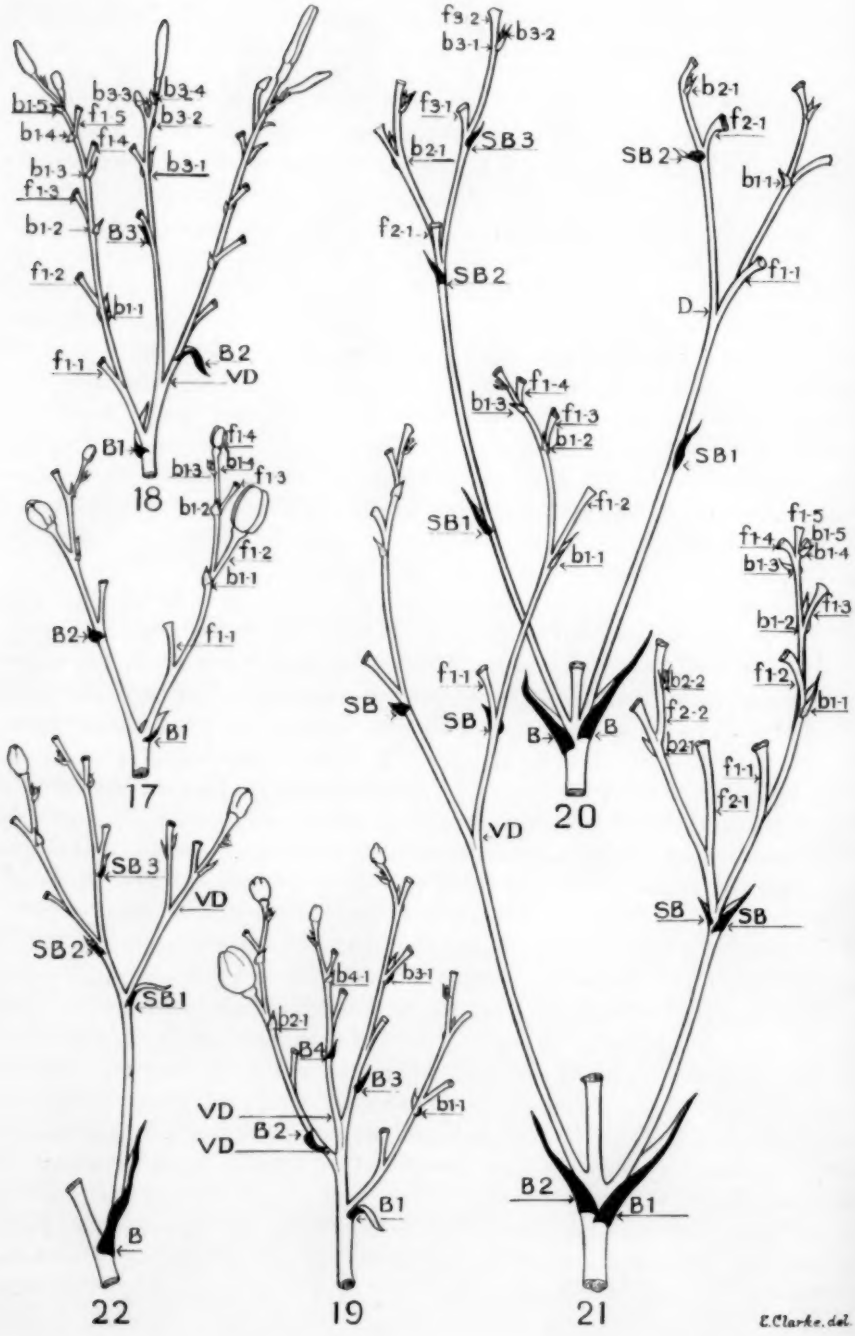
to this a double series with also a spiral arrangement was called a "scorpioid cyme" or "cincinnus."

The dichotomous bostryx. A further modification termed a "dichotomy" was recognized as frequent and characteristic of many genera, especially of monocots, and to exemplify this L. and A. Bravais present a drawing of a branch of the inflorescence of "*Hemerocallis fulva*" (the clone Europa). The essential feature of growth in this is that each new unit of the false axis arises directly from the axis of a flower in a dichotomy in the development of which the bracteole, which belongs at the base of the pedicel of the terminal flower, is transposed to a higher level on the false axis. It may be noted that this feature of "dichotomous" branching may also develop in scorpoid cymes. It is to be recognized that the type of branching that occurs in a bostryx of *Hemerocallis* has been designated (Crozier 1892) a helicoid dichotomy or bostrychoid dichotomy as distinct from the true dichotomy seen in Cryptogams. But in *Hemerocallis* branching at a level where there is neither a node nor a bract occurs both in the development of a bostryx and in the precocious separation of axes that lead into bostryxes. The latter will here be called a vegetative dichotomy.

THE BOSTRYXES IN HEMEROCALLIS

The primary bostryxes or terminal inflorescence. The description of the character of a typical bostryx in *Hemerocallis* will here be combined with a consideration of the interrelation of the two or more bostryxes that combine to form the terminal inflorescence. Also the descriptions will first be for the much branched scapes of the species *H. multiflora*. The slender stems and the rather loosely spaced branches in the scapes of this species somewhat simplify the recognition of the essential features of the dichotomous bostryx and the grouping of bostryxes in the primary and the secondary inflorescences.

Figure 17 shows two primary bostryxes which composed a primary inflorescence below which there were secondary inflorescences that are not shown here. The lower one stands as a lateral in the axil of a primary bract (*B1*) on the main axis of the scape. This lateral begins as a single stem and it definitely continues as such for a distance of almost one inch. Then there is a so-called dichotomy, of which one arm continues as a pedicel of a flower while the other is a single vegetative stem as far as the first bracteole (*b1–1*). Above this bracteole the main axis forms another flower stem in which there is a dichotomy. But this second dichotomy of the bostryx is not far above the bracteole (*b1–1*). The next dichotomy, the third of the series, is only slightly above the level of the next bracteole (*b1–2*) and also its two arms stand side by side in a plane almost parallel to that of the base of the bracteole. Thus the lateral in any "dichotomy" does not stand in the axil of the bracteole below it. Each bracteole stands in a position that is opposite to the pedicel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of the flower below, a feature emphasized by various writers and especially Goebel (1931). The pedicel of the flower below a bracteole (as *f1–1* in fig. 17), the bracteole (*b1–1*), and the lateral unit of the dichotomy below it are all in the positions relative to each other that they would occupy if there were no displacement. There is, however, much twisting of stem units in the main axis and in the various units of a bostryx which breaks the regularity of alignment.

For the uppermost flower of any bostryx, as shown in figure 17, there is an almost single stem which bears the bracteole (see *b1–3*) belonging to the flower below, and close above, but to one side, there is a much smaller bracteole (see *b1–4*). Immediately in its axil there is the aborted terminal end of the false axis, with often a group of small bracteoles, which is lateral to the pedicel of the last flower.

The upper of two bostryxes in a primary inflorescence terminates the main axis of the scape immediately above the uppermost bract (*B-2* in fig. 17) on this axis. *Its first flower is terminal on the main axis of the entire scape.* A lateral on the axis of this flower arises in a bostrychoid dichotomy and the succession of units in the false axis is like that in the lateral bostryx below.

The terminal bostryx, as a rule, is less developed than the one below; its first flower is smaller than is the first flower of the bostryx below and it opens at least one day later; it frequently has at least one less flower in the series.

The internode between the two upper primary bracts, which subtend the two bostryxes that comprise a primary inflorescence, is often noticeably shortened and frequently the lateral to the lower bract is fused with the main axis (figs. 12, 13). But in the species which have most extensively branched scapes this feature is least strongly developed.

It may here be noted that the spiral phyllotaxy of a bostryx may be either clockwise or counter-clockwise, and that the two primary bostryxes of an inflorescence may both be the same in direction or different.

A three-bostryx primary inflorescence of *H. multiflora* is shown in figure 18. The lower two are laterals on the main axis of the scape; the uppermost one is terminal for this axis. As shown in this figure (at *VD*) a vegetative dichotomy frequently develops in the main axis below the primary bract (between *B2* and *B3* of fig. 18) that subtends the middle one of the three bostryxes. Then the primary bract (*B2*) is carried up on the lateral. Each arm of this dichotomy remains a vegetative stem as far as the next bract. In a dichotomy in the bostryx, however, one arm becomes a pedicel of a

Explanation of figures 17–22

FIGS. 17–22. Scapes of *Hemerocallis multiflora;* figures 17, 18, and 19 are primary inflorescences with 2, 3, and 4 bostryxes; figures 20, 21, and 22 show lateral branches below primary inflorescences.

flower. The precocious separation of a lateral from its main axis is a characteristic feature of growth (a) in the bostryx, (b) in the upper part of the main axis of primary inflorescences, (c) in lateral branches of much branched inflorescences (see *VD* in fig. 21), and (d) in at least one species in the first internode (figs. 14, 15) of scapes that are reduced to few flowers.

A four-bostryx primary inflorescence is shown in figure 19. In this there is precocious separation of both the second and the third bostryxes by two successive vegetative dichotomies that occur in the main axis.

The group of primary bostryxes at the apex of a scape constitutes what may be called a primary inflorescence. Occasionally in much branched species there are more than four bostryxes in this group. Always, so it now appears, there are at least two; although in certain species the abortion of one bostryx is frequent in scapes on which only one flower develops to maturity (fig. 16).

The sequence of opening for flowers which occupy corresponding positions in the two or more bostryxes of an inflorescence is almost without exception in succession from the lowest to the uppermost. The dominance in vigor of a lower bostryx to the bostryx above it is conspicuous and almost universal for all inflorescences in all species of *Hemerocallis*. This aspect of growth is also seen when a lateral develops immediately below the terminal in the simpler inflorescence of *H. nana*.

Secondary inflorescences. The secondary inflorescences of *H. multiflora* here shown in figures 20, 21, and 22 exemplify several of the features characteristic of the laterals that develop below the primary inflorescence, especially in species that are rather freely branching. The axis of a secondary inflorescence usually has one or more vegetative internodes for each of which there is a secondary bract (*SB* in figs. 20, 21, and 22). There are usually at least two terminal bostryxes in a secondary inflorescence. The internode between the two bracts may be short (see right branch in fig. 21); it may be quite elongated with the lateral arising in a dichotomy (*D* in fig. 20); or a dichotomy may arise in the main axis below the bract that subtends the first bostryx (*VD* in figs. 14, 15, and 21). In figure 22 is shown a lateral which has a primary inflorescence of two bostryxes below which there is a secondary lateral (to *SB1*) with a dichotomy and two bostryxes. In these the lateral bostryx has only two flowers, and the terminal one has but one flower.

THE INFLORESCENCE OF H. FULVA CLONE EUROPA

The dichotomous bostryx of the Europa daylily was illustrated and described by L. and A. Bravais (fig. 10) and frequently since referred to as exemplifying the "uniparous" helicoid cyme or bostryx. But this illustration is only for a lateral of the two or more bostryxes which form a primary inflorescence. Figure 11 shows a typical two-bostryx inflorescence of this widely cultivated clone at the time when its first flower is ready to open.

Both the dominance in the growth and development of the lateral bostryx and the dichotomous separation of each new lateral segment of the false axis are here well shown. At the conclusion of flowering a two-bostryx inflorescence often appears as in figure 12, and a three-bostryx inflorescence as in figure 13. The interpolation of the axes of the three bostryxes is evident in the segment above the lower primary bract (see *B1*).

In many scapes of plants of this clone only the two or more primary bostryxes are developed and the one or more primary bracts below have no laterals. When there are secondary inflorescences these are placed next below the terminal group of bostryxes and are relatively less strongly developed. The character of the scape of the Europa daylily is quite typical for the species *H. fulva*, which is widely distributed in Asia. In comparison with *H. multiflora* the scapes of the Europa daylily are coarser, and the lateral branches below the primary inflorescence are more often absent or weakly developed.

In the scapes of both *H. fulva* clone Europa and *H. multiflora* it is the rule that there are more than two internodes in the main axis of a scape and that a dichotomy is not seen in the main axis below a primary inflorescence. However in those scapes of *H. minor* which are reduced to only two rather small primary bostryxes there is frequently a vegetative dichotomy in the upper part of the first internode below the level of the first bract (figs. 14, 15).

CONCLUDING REMARKS

The conceptions of the nature of the bostryx or uniparous helicoid cyme, the descriptions of it, and the terms applied to it as presented by the early writers (Schimper according to Braun 1835; and L. and A. Bravais 1837) have been fully endorsed by such later writers on the morphology of inflorescences as Hofmeister (1868), Sachs (1875), Eichler (1875), Bessey (1885), Goebel (1887, 1931), and Velenovsky (1910). Even in the more complicated dichotomous bostryxes, as in *Hemerocallis*, it has been recognized by these authorities that each flower is truly terminal and that the axis of a succession of flowers is composed of a series of false axes each unit of which arises as a lateral. Yet there are recent monographs dealing with the classification of the genus *Hemerocallis* which unreservedly state, without mention of the helicoid and cymose nature of the branches, that the inflorescence is a panicle (Hutchinson 1934) or that its character ranges from racemose to paniculate (Nakai 1932). It is to be noted that the term inflorescence, as well noted by Parkin (1914), is sometimes applied to the mode of floral branching, at other times applied to the flower cluster itself, and at other times it refers to both of these conditions.

In *Hemerocallis*, within each bostryx the flowering is determinate and hence cymose. For the primary group of bostryxes the sequence of development is racemose. This is, evidently, what the term panicle has come to

include in the description of the inflorescences in many genera. In *Hemerocallis* the helicoid cyme or bostryx is to be recognized as a unit branch in the inflorescence.

In *Hemerocallis* the consideration of the bostryx refers to the arrangement of flowers in a single flowering branch that may arise in the axil of a bract or terminate a main axis above its last bract. In a bostryx, each flower is terminal for its axis below and its dichotomous lateral continues as a false axis which finally ends in an abortion, and on which the flowering sequence is that of a false raceme.

In all species except *H. nana* two or more bostryxes at the apex of the scape constitute what may be called a primary inflorescence. In the relative development of these bostryxes a lateral one is dominant over the terminal one for the main axis and thus the sequence in the development of these branches is racemose. The same relation in development exists in the group of two or more bostryxes that may terminate any lateral that is below the primary inflorescence.

Thus there is one fundamental feature of growth in the inflorescence that is common to all the species of *Hemerocallis*. In *H. nana* many scapes have two flowers, one terminal on the main axis and one terminal on a lateral, and in all other species at least two bostryxes combine to form a terminal inflorescence. In both cases the lateral dominates in size, vigor of growth, and time of development. The flowering of the central or main axis and of the laterals is determinate and the sequence of development is centripetal. It is the development of branches from the pedicels, in all species except *H. nana*, and their precocious separation by dichotomy that give the false axis and the racemose appearance of the bostryx in *Hemerocallis*.

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THE ONTOGENETIC DEVELOPMENT AND PHYLOGENETIC SPECIALIZATION OF RAYS IN THE XYLEM OF DICOTYLEDONS—III. THE ELIMINATION OF RAYS[1]

ELSO S. BARGHOORN, JR.

(WITH FOURTEEN FIGURES)

Extensive study[2] of the ontogeny and phylogenetic specialization of rays reveals that ray tissue may be completely eliminated from the secondary xylem. The process of ray elimination is not an isolated phenomenon, but occurs in a wide range of dicotyledonous shrubs and semi-shrubs. The absence of rays is correlated with reduction in cambial activity and often with a tendency toward the herbaceous habit of growth. In addition, the rayless condition occurs in many shrubs and suffruticose forms possessing anomalous secondary thickening, included phloem, successive cambia, etc. A conspicuous suppression, though rarely complete absence, of rays may be observed in many plants which have undergone dwarfing or modifications in relation to xerophytic or otherwise unfavorable environments. The various ontogenetic changes which effect the elimination of rays are emphasized in this study; in addition, however, the relation of ontogeny to phylogeny is considered.

Kribs' investigations on the structural specialization of rays in dicotyledons do not include data on the elimination of rays (Kribs 1935). However, from previous studies by the writer (Barghoorn 1940, 1941) it is evident that the loss of rays results in a highly specialized condition. Additional evidence for this is afforded by the fact that rayless structure occurs in a wide range of unrelated families (figs. 1–6, 7, 9, 10), and is usually associated with a high degree of general structural specialization.

From Kribs' study, supported by the writer's investigations, there are two major trends of specialization of ray tissue in dicotyledons. These are the elimination of uniseriate rays to leave multiseriate rays only, and the elimination of multiseriates to leave uniseriates only. Both of these trends are usually associated with changes in the morphology of the ray cells. In the rayless forms and those with poorly developed rays the tendency towards the elimination of both types of rays coincides with the reduction in secondary growth. It has been shown in earlier papers of this series that phylogenetic modification of ray structure may be initiated in either the early or the later stages of ontogeny of the secondary body. In the elimination or extreme reduction of rays, however, phylogenetic specialization proceeds

[1] The first paper of this series appeared in Am. Jour. Bot. 27: 918–928. 1940. The second paper will appear in Am. Jour. Bot. for April, 1941.

[2] In this series of investigations various species from 195 families of dicotyledons were examined from the extensive slide and wood collections of Harvard University.

from the early to the later stages of development rather than vice-versa. That is, phylogenetically the rays are lost from the inner secondary xylem before their elimination from the outer parts of the secondary body. This is indicated by the fact that in many shrubs and semi-shrubs rays are absent from the inner portions of the woody cylinder while present in varying numbers in the outer portions (figs. 7, 8). No well developed rays have been observed in the inner secondary xylem of species devoid of rays in the outer. Moreover, frequently the vestiges or "ghosts" of rays may be observed in transverse sections, while radial or tangential longitudinal sections show conclusively that rays are absent (figs. 1, 2, 3, 9). From these facts it is quite clear that the elimination of ray tissue is a morphological modification which is the reverse of the so-called recapitulation phenomenon. This is evidenced by the fact that the ancestral condition, viz., the presence of rays, is represented in the later stages of development rather than in the early stages.

From the standpoint of ontogenetic development the phylogenetic specialization of rays is accomplished by a consecutive series of increasingly modified ontogenies. In the loss of rays the tendency for elimination is expressed, ontogenetically, at increasingly later stages of development until eventually the secondary xylem is entirely devoid of rays. Various stages in the ontogenetic-phylogenetic elimination of rays are similar in clearly unrelated groups of dicotyledons. They therefore represent similar, parallel trends of phylogenetic specialization brought about by similar ontogenetic changes.

THE ELIMINATION OF RAYS BY THE ENLARGEMENT OF RAY INITIALS

Various complex cellular changes characterize the development of rays in the cambium (Chattaway 1933, Barghoorn 1940, 1941). Among these is the transformation or reversion of ray initials to the fusiform type of cambial cell. If such a transition is localized and definitely oriented within a multiseriate ray the elongating initials split or dissect the ray into two or more separate portions as illustrated in figure 7 of the second paper of this series. If, however, the tendency for elongation affects all the ray initials, the ray tends to lose its distinct morphological identity, since its constituent cells may resemble in size and shape the cells of the surrounding tissue (figs. 8, 11). For the sake of completeness it should be pointed out that ontogenetically such extensive change in all the initials of a ray seldom occurs during development of the secondary xylem of an individual. If a phylogenetic series is studied, however, it becomes clear that the degree of emphasis on ray initial elongation, at different stages, results in the partial or complete elimination of the rays as distinct structures.

The majority of species in which rays are in course of elimination by the enlargement of initials do not possess uniseriate rays. In these, therefore, the

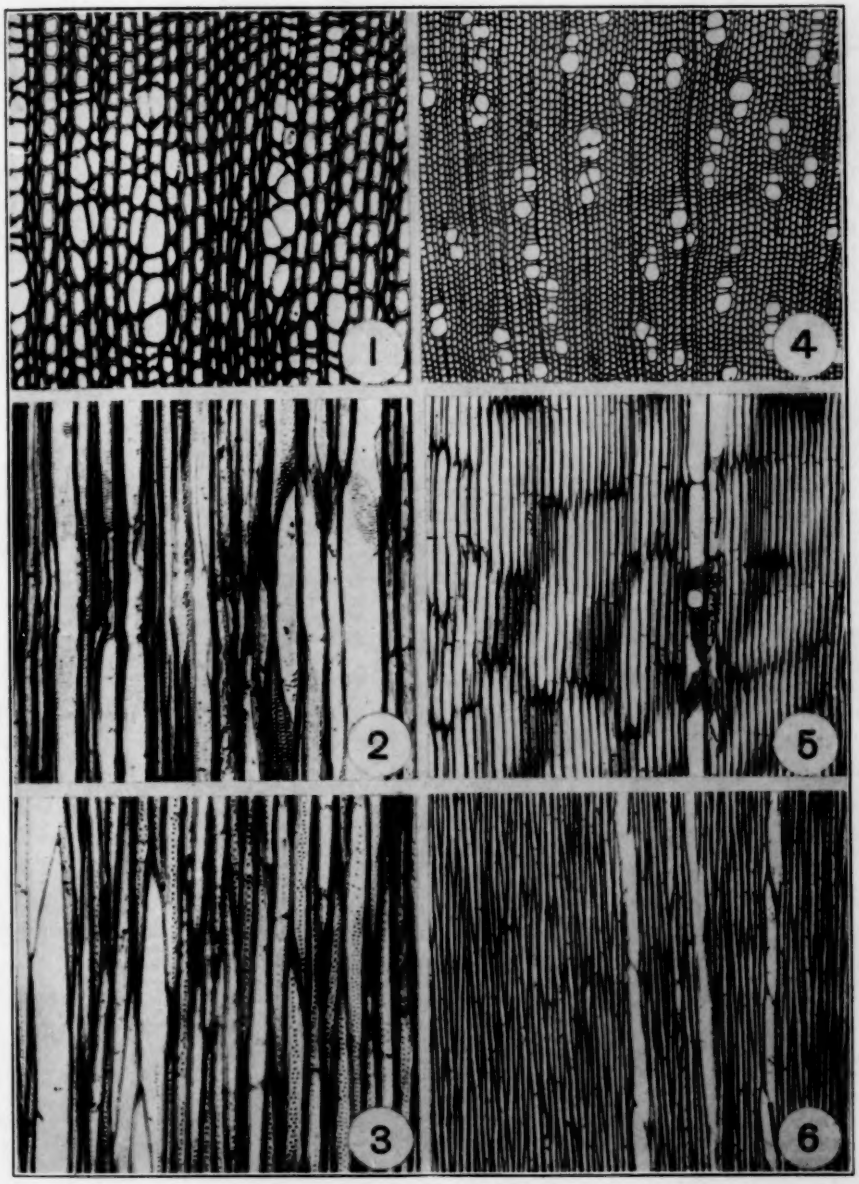


FIG. 1. *Alseuosmia macrophylla* Cunn. (Caprifoliaceae). Transverse section of the secondary xylem. Note the absence of rays. The radial rows of smaller cells represent the "ghosts" of rays which have been eliminated (×125). FIG. 2. *Alseuosmia macrophylla.* Radial longitudinal section indicating, similarly, the absence of rays (×125). FIG. 3. *Alseuosmia macrophylla.* Tangential longitudinal section showing the rayless secondary xylem. Compare with figs. 1 and 2 (×125). FIG. 4. *Besleria* sp. (Gesneriaceae). Transverse section showing secondary xylem completely devoid of rays. In this species wood parenchyma is nearly absent and the secondary xylem consists almost entirely of vessels, libriform fibers, and septate fibers (×40). FIG. 5. *Besleria* sp. Radial longitudinal section showing the rayless secondary xylem in longitudinal view (×40). FIG. 6. *Besleria* sp. Tangential longitudinal section. Note the complete absence of rays. Compare with figs. 4 and 5 (×40).

majority of the ray tissue consists of heterogeneous multiseriate rays of varying size, composed of large, more or less vertically elongated cells, as shown in figures 8 and 11. Occasionally uniseriate rays are present as well, but these are likewise composed of vertically elongated cells. Heterogeneous multiseriate rays such as occur in the early stages of the elimination of rays should not be confused with the heterogeneous multiseriates of the primitive ray structure. The specialized multiseriate rays occur in species which usually exhibit a high degree of structural specialization of the secondary xylem. Their cells frequently appear irregular and angular when viewed in tangential longitudinal sections and commonly possess thin secondary walls which are devoid of the abundant, conspicuous, simple pitting found in primitive multiseriate rays (fig. 11).

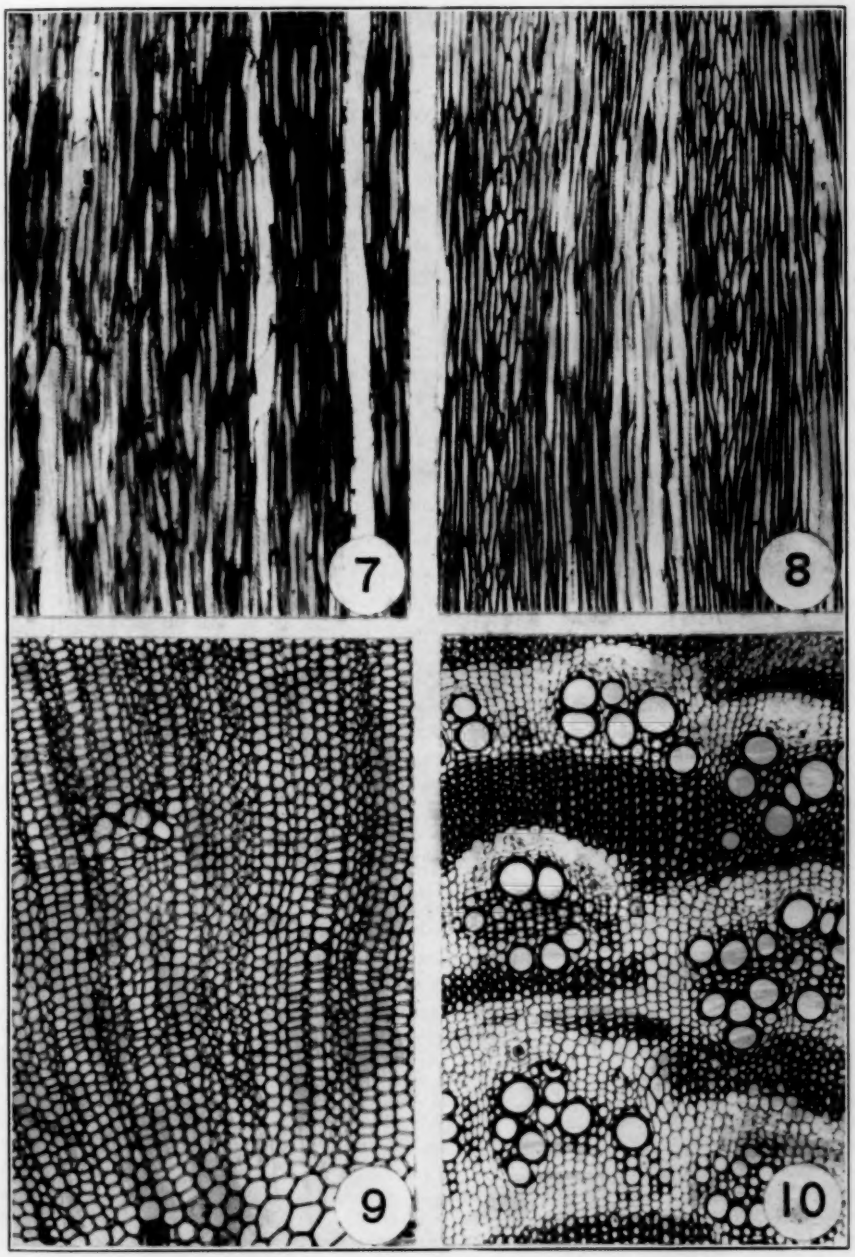
Interestingly enough, the phylogenetic elimination of rays by the progressive increase in the size of ray initials brings about their loss by expansion rather than reduction. In other words the rays are eliminated by the "overdevelopment" rather than suppression of their initials.

REDUCTION OF RAYS BY THE SUPPRESSION OF RAY INITIALS

In strong contrast to the elimination of rays by the enlargement of their initials is the reduction of ray tissue by the suppression of ray initials in the cambium. As has been previously noted, this condition is found chiefly in dwarfed plants, of suffruticose habit, growing in xerophytic or otherwise unfavorable environments. Not only is cambial activity reduced in such plants but the size of the cambial initials is often reduced far more than would be anticipated from the degree of phylogenetic specialization of the vessel elements. Shrubby forms such as these therefore exhibit strong tendencies toward similar anatomical modifications even though they may differ widely in the extent of structural specialization of the secondary xylem, or in their floral morphology.

Explanation of figures 7–10

FIG. 7. *Geranium tridens* Hbd. (Geraniaceae). Tangential longitudinal section of inner secondary xylem indicating the absence of rays in the early stages of development of the secondary xylem. Phylogenetically the ray initials in the early stages have elongated to the fusiform type of cambial cell (×95). FIG. 8. *Geranium tridens.* Tangential longitudinal section of outer secondary xylem of same stem indicating the presence of high-celled multiseriate rays in the later-formed secondary xylem. Phylogenetic modification has not yet resulted in the elimination of rays in the later stages of development of the secondary xylem (×95). FIG. 9. *Sempervivum arboreum* L. (Crassulaceae). Transverse section showing portions of the pith and the rayless early secondary xylem. Note the "ghosts" of multiseriate rays extending outward from the pith. Tangential and radial longitudinal sections show that the woody cylinder is completely devoid of rays (×95). FIG. 10. *Frankenia grandiflora* Ch. and Schl. (Frankeniaceae). Transverse section of secondary xylem of a root showing secondary thickening by means of successive cambia. Note the complete absence of rays, a condition characteristic of this type of structure (×95).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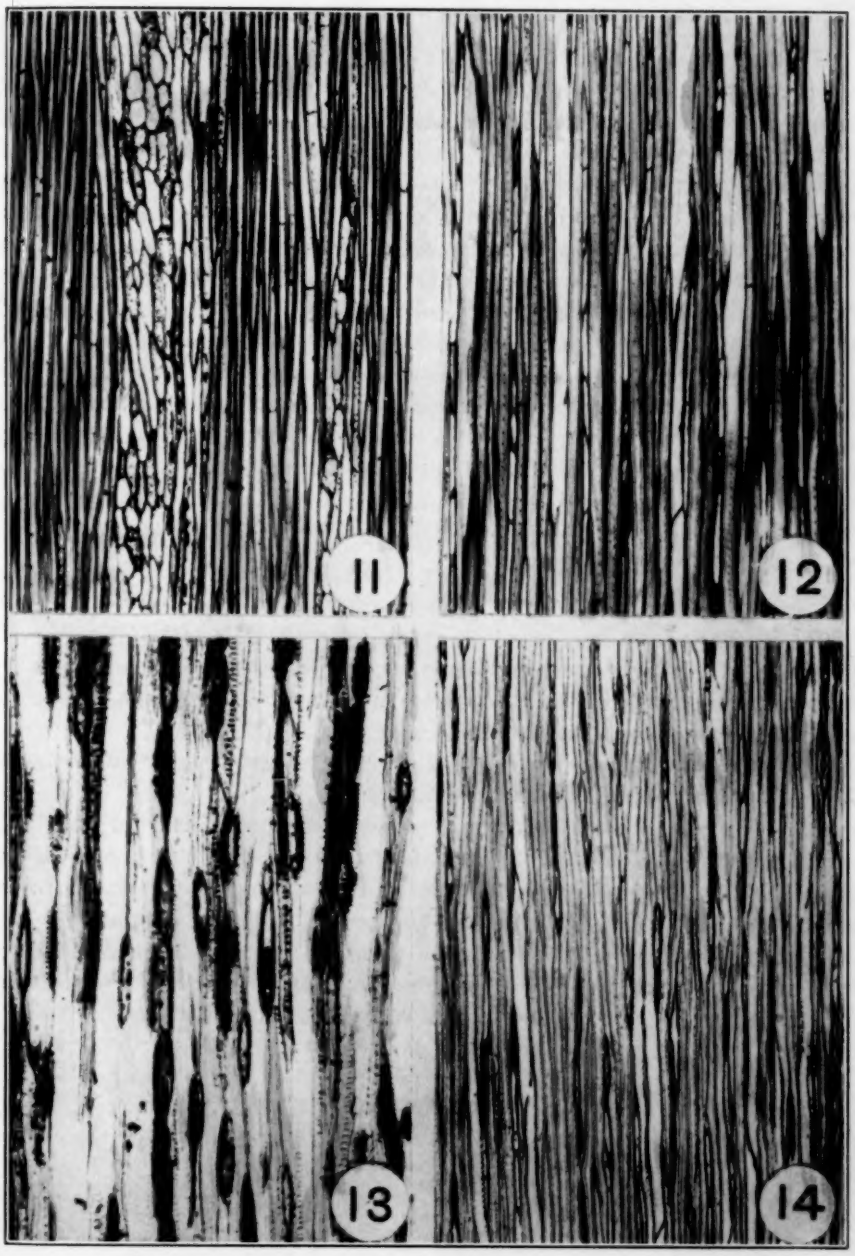
The influence of dwarfing on the ray tissue of the secondary xylem usually affects the height and width as well as the number of rays (Forsaith 1920). Commonly the multiseriate rays are eliminated and the uniseriate rays reduced in height (figs. 13, 14). Frequently the uniseriate rays are composed of vertically elongated cells only (figs. 12, 13, 14). Further reduction of the ray tissue tends to produce rays extended by solitary initials or by uniseriate strands of initials from three to four cells high. In extreme cases of reduction the xylem ray cells are somewhat disjunctive and therefore not radially contiguous. In certain members of the Cistaceae the innermost secondary xylem is devoid of rays while the outer parts possess only one-celled uniseriate rays of the disjunctive type.

As in the elimination of rays by cell enlargement, the tendency for suppression of rays affects first the early stages of secondary growth. This is apparently true regardless of the degree of structural specialization of the xylem or the extent to which the ray tissue is reduced. Thus in many species the multiseriate rays have been eliminated from the inner secondary xylem leaving high-celled uniseriates only, whereas in the outer secondary xylem both multiseriate and uniseriate rays are present. Similarly, if only reduced uniseriate rays are formed throughout the secondary xylem, they are frequently less numerous in the early stages of development and composed of cells which are more elongated vertically than ray cells in the later stages.

It should be emphasized that in the elimination or reduction of rays there is not a phylogenetic trend from heterogeneity to homogeneity. Rather, the reverse is true, particularly of rays being eliminated by cell enlargement, inasmuch as ray initials and their daughter cells progressively increase in the vertical dimension instead of becoming more nearly isodiametric. The anatomical modifications which characterize the reduction or elimination of rays are identical in both roots and stems. There is no significant difference in the ontogeny or the rate of phylogenetic specialization of ray tissue in the two major portions of the plant.

Explanation of figures 11–14

FIG. 11. *Ardisia Brackenridgei* (A. Gray) Mez. (Myrsinaceae). Tangential longitudinal section of secondary xylem showing the tendency to loss of rays by the vertical elongation of ray initials. (×95). **FIG. 12.** *Staavia glutinosa* (l.) Thbg. (Bruniaceae). Tangential longitudinal section illustrating the tendency to reduction of rays by suppression of them in the cambium. Multiseriate rays have been eliminated and the uniseriate rays are composed solely of vertically elongated cells (×95). **FIG. 13.** *Corema Conradii* Torr. (Empetraceae). Tangential longitudinal section showing marked reduction of ray tissue. Note that many of the rays are reduced to the one-celled uniseriate condition (×230). **FIG. 14.** *Tetratheca ciliata* Lindl. (Tremandraceae). Tangential longitudinal section illustrating reduction of ray tissue similar to that shown in figs. 12 and 13. The plants represented in figs. 12, 13, and 14 all exhibit conspicuous morphological as well as anatomical reduction (×95).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ANOMALOUS SECONDARY GROWTH AND THE LOSS OF RAYS

In many species of dicotyledons, particularly in the Centrospermae, secondary thickening occurs by the activity of successive cambia. In such plants, particularly if secondary growth is rather limited, the woody cylinder is commonly devoid of ray tissue (fig. 10). In some species, in the innermost secondary xylem, and before the formation of supplementary cambia, rather poorly defined, high-celled multiseriate rays may be developed. These, however, are not continuous across the arcs of included phloem which are subsequently formed. Similarly, in the broader zones of uninterrupted secondary xylem of later stages, high-celled multiseriate rays may be produced, but these too are transitory and therefore do not constitute normal ray tissue.

It is quite clear that the formation of successive cambia and included phloem is not a stage in the phylogenetic modification of rays. However, it is an anatomical modification which is closely associated with a loss of ray tissue and commonly results in the complete elimination of rays.

SUMMARY

1. Extensive study of the anatomy of dicotyledons reveals the fact that ray tissue may be completely eliminated from the secondary xylem.

2. The absence of rays is a highly specialized condition, associated with reduction of cambial activity and in many cases with a tendency toward the herbaceous habit of growth. The rayless condition also occurs in many plants possessing anomalous secondary thickening.

3. The elimination of rays is accomplished phylogenetically by the transformation of ray initials to fusiform initials.

4. Conspicuous reduction, though rarely complete absence of rays may result in plants which have undergone dwarfing or extensive modifications in relation to xerophytic or otherwise unfavorable environments. In these cases the formation of ray initials is suppressed in the cambium.

5. Phylogenetically, the elimination of rays is initiated in the early rather than in the later stages of development of the secondary xylem. The tendency for loss of rays is extended, phylogenetically, into successively later stages of ontogeny until the woody cylinder is devoid of ray tissue.

The writer wishes to express his appreciation to Professor I. W. Bailey for his interest and assistance in this study.

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NOTES ON APHANIZOMENON WITH A DESCRIPTION OF A NEW SPECIES[1]

EDWARD G. REINHARD[2]

(WITH FIVE FIGURES)

Aphanizomenon is a familiar blue-green alga common in the plankton of quiet waters, often forming a heavy bloom on the surface of ponds and lakes during the summer and early autumn. Its plate-like bundles of agglutinated trichomes are very noticeable to the unaided eye, appearing like small bits of cut grass.

Only a single species, *Aphanizomenon Flos-aquae* (L.) Ralfs, has heretofore been reported from the United States. This alga is so abundant at times that it dominates the plankton and gives the water a semblance of green paint. In a bay at the eastern end of Lake Sakatah in southern Minnesota the writer observed a vast mass of *Aphanizomenon*, probably concentrated by the wind. The water contained *Aphanizomenon* filaments to the number of 2,500,000 per cc. Associated with this species were colonies of *Microcystis aeruginosa* Kuetz. numbering 600 per cc. This dense population of algae increased the dissolved oxygen content of the water to supersaturation on October 15, 1929, when this observation was made; the water temperature was 22° C.

The generic description of *Aphanizomenon* given by most phycologists includes the statement that the spores (akinetes) are solitary. Yet Schmidle (1897) described a species possessing 1–3 spores in series. This species, which he called *Aphanizomenon Kaufmanni*, is recognized as a true representative of the genus, but phycologists in general have neglected to revise the generic description to include the species with seriate spores.

This neglect was mainly due to the fact that the description of the new species remained virtually unknown for a long time after publication, no doubt because it was incorporated in an article by P. Kaufmann which appeared in an obscure publication, *Revue d' Égypte*, a publication which is now almost inaccessible. In 1914, however, Brunnthaler in *Hedwigia* brought Kaufmann's article to the attention of botanists by publishing a brief abstract of it and reprinting Schmidle's Latin diagnosis of the species together with the original figures. The species is also described, but not figured, by Geitler (1925). It is one of the organisms chiefly responsible for the so-called "green water," an annual phenomenon of the Nile.

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[1] Contribution from the Department of Biology, The Catholic University of America, Washington, D. C.

[2] The author is indebted to Prof. J. E. Tilden for assistance in this study, which was begun in the Botanical Laboratories of the University of Minnesota.

While investigating the plankton of the upper Mississippi River and its tributaries (Reinhard 1931), I came upon an *Aphanizomenon* which is strikingly different from *A. Flos-aquae* and resembles the species which Schmidle described from the Nile. It appeared in the plankton of the Minnesota River and was so abundant that it imparted to the concentrated plankton sediment a very noticeable blue-green color, which was even apparent, though much less distinct, in the unconcentrated water. The sample from the Minnesota River was taken at Mendota on July 31, 1928, from a depth of five feet in mid-channel. This species was found in association with other algae as follows:

Aphanizomenon sp. nov.	22,200	individuals	per	cc.
Melosira granulata	186	"	"	"
Gyrosigma Spenceri	42	"	"	"
Green flagellates	96	"	"	"

In the Mississippi River likewise, below its confluence with the Minnesota, this *Aphanizomenon* was present in the plankton as far down as the head of Lake Pepin. Above the Minnesota it did not occur at all. The numbers, however, progressively diminished in the Mississippi water, and it is apparent that the *Aphanizomenon* originated and developed in the Minnesota and was contributed to the Mississippi plankton by the tributary water.

The Minnesota is a broad, slow-moving stream with scarcely any slope in the last fifty miles of its course. It occupies a wide valley, the bottom lands marshy and fringed with ponds. It is probable that the *Aphanizomenon* originated in these marshes.

The month of July was a period of relatively low water with high temperatures. During this period the temperature of the Minnesota River was 26° C., the warmest record for the year.

Like the *Aphanizomenon* of the Nile, the Minnesota species was short-lived as a plankton constituent. The following table gives the only occurrences of this peculiar species throughout the 1928 plankton investigation, although collections were made every two weeks from February to October.

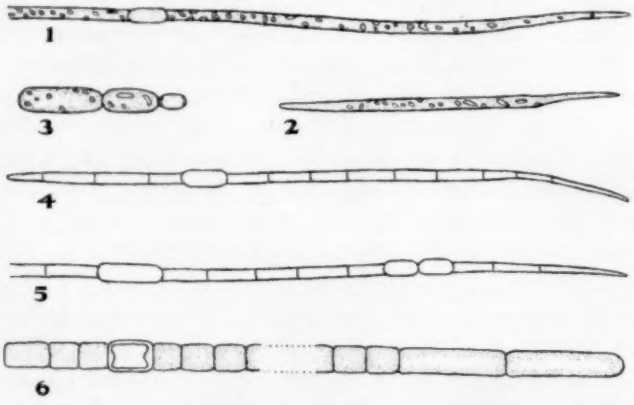
TABLE 1

Stations	Miles below Minnesota River	Date	Water temperature °C.	*Aphanizomenon* filaments per cc.
Minnesota River at mouth	0	July 31	23	22,200
Mississippi R. at Inver Grove	15	July 31	23	1,200
Mississippi R. at Hastings	33	Aug. 2	22	530
Mississippi R. at Red Wing	55	Aug. 1	24	465

This alga, allied to *A. Kaufmanni,* appears to be a new species. I propose to name it *Aphanizomenon americanum,* since it is the first species of *Aphanizomenon* to be described from the United States.

Aphanizomenon americanum Reinhard, sp. nov. Filamentis solitariis aut in laminulis tenuiter inter se coniunctis, rectis aut quasi curvatis vel prope sigmoideis, aerugineis, ad 200 μ longis, ad disseptimentes vix visibiles non constrictis; trichomatibus ad unum aut utrumque apicem elongatis quasi caudatis; apicibus ex 1–3 cellulis tenuibus formatis, cellulis apicalibus ad 16 μ longis, cellulis vegetativis cylindricis, 2–3 μ latis, 6–13 μ longis, pseudovacuolis rubris. Sporis singulis aut duobus contiguis, elongatis, fere cylindricis et utrimque rotundatis, 3–5 μ latis, 6–13 μ longis, intus quasi granulosis. Heterocysta (solam unam vidi) longe elliptica, 2.6 μ lata, 3.5 μ longa, sporis proxima.

Plant mass floating; trichomes 100–200 μ in length, solitary or loosely united in thin plate-like bundles, straight, slightly curved or nearly sigmoid, tapering at one or both ends into caudate extensions of 1–3 apical cells, not constricted at the joints, blue-green in color with reddish pseudovacuoles. Vegetative cells cylindrical, 2–3 μ in diameter, 6–13 μ in length, narrowed apical cell sometimes reaching a length of 16 μ. Akinetes 3–5 μ in diameter, 6–13 μ in length, single or geminate, subcylindrical, elongate, rounded at both ends; cell contents granular. Heterocyst (I have seen but one) 2.6 μ in diameter, 3.5 μ in length, somewhat elliptical, situated adjacent to the akinete.



FIGS. 1–5, *Aphanizomenon americanum* Reinhard. FIG. 6, *Aphanizomenon Flos-aquae* (L.) Ralfs, drawn to same scale for comparison. All × 900. FIG. 1, typical appearance of trichome. FIG. 2, young sterile trichome. FIG. 3, two large akinetes with a heterocyst above. FIGS. 4, 5, trichomes with akinetes, drawn to show cell walls.

A comparison between Schmidle's description of the *Aphanizomenon* of the Nile and the description which I have just given of the Minnesota plant does not appear at first glance to bring out any clear-cut distinctions between the two. This is partially due to the limitations of language and to the brevity of the earlier description. But if the drawings of the two forms are used to illustrate the meanings of the words employed it becomes evident at once that significant differences do exist. Only an exact comparison of actual specimens can, of course, positively demonstrate every point of dissimilarity.

Aphanizomenon americanum appears to differ from *A. Kaufmanni* Schmidle in the following respects:

A. Kaufmanni	*A. americanum*
One attenuated apical cell.	A series of attenuated cells at the apices.
Apices sometimes twisted spirally.	Apices always straight.
Length of heterocyst at least twice the diameter.	Length of heterocyst less than twice the diameter.
Akinetes somewhat elliptical.	Akinetes with sides practically parallel.

The septa separating the cells of *A. americanum* are not discernible unless special methods are employed to demonstrate them. Staining the trichomes with an aqueous solution of neutral red works well on material preserved in formalin and brings out the transverse septa very clearly.

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A NEW CYPERACEOUS GENUS FROM NORTHERN SOUTH AMERICA

CHARLES GILLY

Floristic and taxonomic studies have revealed the presence of a great number of endemic genera in the Sierra Pacaraima, an ancient mountain complex along the Venezuela–Brazil–British Guiana boundary. The botanical collections of Mr. G. H. H. Tate from Mt. Roraima, Mt. Duida, and Mt. Auyan-tepui have been the basis for the description of many of these endemics. Among his collections were specimens of dioecious Cyperaceae which are here recognized as an addition to the list of endemic genera of this area. Dioecism, of itself, cannot of course be regarded as a generic character in the Cyperaceae, but dioecism together with a sufficient number of habital characters can serve as an indicator of generic difference.

Böckler (1) in 1874 described *Cryptangium stellatum* on the basis of a pistillate plant, *Schomburgk 1227*, from British Guiana; the exact collection locality of this specimen is not given, but it quite certainly is somewhere near Mt. Roraima. *C. stellatum* differed from other members of the genus not so much in its dioecious character, for there were already other known dioecious species of *Cryptangium*, as by the arrangement of its leaves and inflorescence. The staminate plant of the species was described in 1886 by Ridley (5); both Ridley's description and the figure which appeared in 1887 (7) were based on *im Thurn 357* from Mt. Roraima. Ule also collected staminate plants from Mt. Roraima (6), and I have previously reported (3) the staminate collection made by Tate on Mt. Auyan-tepui. Among the specimens referred to the genus "*Everhardia*" by Britton in the Duida report (2) was *Tate 542*, which I have already excluded from *Everardia* (4); comparison of this specimen with the Tate specimens of *Cryptangium stellatum* from Mt. Auyan-tepui leaves little doubt that, despite their superficial dissimilarity, they are congeneric. Inasmuch as I am convinced that they represent a separate genus, distinct from and not at all closely related to *Cryptangium*, I propose for them the following name:

DIDYMIANDRUM[1] GILLY, GEN. NOV.

Herba perenna terrestris vel epiphytica dioica; culmi rhizomati lignosi erecti triangulares; folia conferta subverticillatim terna disposita persistentia; vaginae rigidae truncatae; inflorescentia multipaniculata multiramosa multispiculata interrupta, paniculae singulares in tertia quaque axilla; spiculae masculae geminae vel rare solitariae vel tres simul, glumis

[1] Derived from two Greek words meaning *twin* and *male*, in reference to the usually paired staminate spikelets.

exterioribus vacuis 5–8, glumis interioribus fertilibus 2–8; stamina a gluma fertili subtenta 2–3, fllamentis persistentibus; spiculae foemineae 1-florae solitariae vel rare geminae, glumis 5–?; achaenium triangularium tricostatum apice rostrato; perianthio trifido, lobis bifidis ciliolatis; stylo trifido.

TYPE SPECIES: *Cryptangium stellatum* Böckl.

Didymiandrum is most closely related to the genera *Everardia* and *Cephalocarpus*, both of which are Sierra Pacaraiman endemics, and with them is referable to the tribe Lagenocarpeae.[2] *Didymiandrum* may be most easily separated from these other two genera by its dioecious inflorescence and the subverticillate arrangement of its leaves.

KEY TO THE SPECIES[3]

Leaves lanceolate to lanceolate-elliptic, 5–18 cm. long, 2.5–4 cm. wide, either entirely glabrous or glabrous except for the white-ciliate margins ..... 1. *D. stellatum*

Leaves narrowly linear, 15–25 cm. long, 1.5 mm. or less in width, minutely soft-pubescent on both surfaces ..... 2. *D. flexifolium*

1. **Didymiandrum stellatum** (Böckl.) Gilly, comb. nov. *Cryptangium stellatum* Böckl. Linnaea **38**: 421. (descr. plantae ♀). 1874; descr. ampl. Ridley, in im Thurn, Timehri **5**: 209. (descr. plantae ♂). 1886. *Acrocarpus stellatus* Nees; Böckl. Linnaea **38**: 421 (in synonymy). 1874. *Lagenocarpus stellatus* (Böckl.) Kuntze, Rev. Gen. 754. 1891.

Culmi stricti ad 1 m. alti; folia lanceolato-elliptica vel lanceolata plana omnino glabra vel glabra praeter margines ciliolatos, 5–18 cm. longa, 2.5–4 cm. lata; culmus quisque floriferus multiramosus, cum inflorescentia ad 20 cm. altus; spiculae masculae ad 6 mm. longae, glumis vacuis 6–8 ovatis vel lanceolatis mucronatis 1–2 mm. longis, glumis fertilibus 2–4 lanceolatis acutis vel acuminatis ad 4 mm. longis; spiculae foemineae subturbinatae ad 3–4 mm. longae, glumis 5 ovatis inferioribus cuspidatis superioribus mucronatis; achaenium obtuse triangulare tricostatum ad basim obovatum, apice rostrato attenuato subtruncato; perianthio trifido, squamis bifidis ciliolatis; stylo brevi, stigmatibus 3.

Specimens examined: VENEZUELA–BOLIVAR: Mt. Auyan-tepui, 2200 m., Dec. 1937, *Tate 1348* (NY). Also reported (5, 6, 7) from Mt. Roraima.

2. **Didymiandrum flexifolium** Gilly, sp. nov. Planta mascula: Rhizomati ad 3 mm. diam. et 30 cm. alti; folia linearia acuta persistentia pubescentia plana praeter apicem bicarinatum, 15–25 cm. longa, 1.5 mm. minusve lata; culmus quisque floriferus rigidus erectus, cum inflorescentia 5–15 cm. altus; spiculae masculae 5 mm. longae, glumis vacuis 5 ovatis subbifidis mucronatis ad 1 mm. longis, glumis fertilibus 6–8 lanceolatis acutis 4–5 mm. longis. Planta foemina et achaenium ignota.

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[2] This tribe is usually called the Cryptangiae, but because of the doubtful status of the genus *Cryptangium* I am following Pfeiffer in the choice of a tribal name.

[3] Specimens examined in this study are deposited in the herbarium of the New York Botanical Garden (NY), and in the United States National Herbarium at Washington, D. C. (US).

Specimens examined: VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, epiphytic on bark of tree, flat near stream at Central Camp, 4800 ft., Dec. 20–28, 1928, *Tate 542* (NY, TYPE; US).

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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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